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VARIATION AND DIFFERENTIATION IN CERATOPHYLLUM.

BY

RAYMOND PEARL

WITH THE ASSISTANCE OF

OLIVE M. PEPPER AND FLORENCE J. HAGLE

WASHINGTON, D. C.:
Published by the Carnegie Institution of Washington
February, 1907

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VARIATION AND DIFFERENTIATION IN CERATOPHYLLUM.

By RAYMOND PEARL,

With the assistance of OLIVE M. PEPPER and FLORENCE J. HAGLE.

INTRODUCTION.

The purpose with which this investigation was undertaken was to attempt to work out as exactly and completely as possible for a particular organism the laws according to which post-embryonic differentiation and growth occur. In higher plants and animals the phenomena of growth are accompanied by phenomena of differentiation. The two processes go along together until finally the adult condition is reached, in which the organism has attained not only a certain size, but also a complex condition of differentiation of parts or organs. In studies of variation it has been the usual—though by no means invariable—custom to take a particular character or set of characters found in the adult as something given, and then proceed, by processes now becoming well known, to investigate the nature and degree of the variation exhibited in these characters. But since the condition of the adult organism is, with respect to every character, the result of a process of gradual development and growth, it is clear that in order to gain anything approaching a satisfactory analysis from the biological standpoint, we can not take the adult structure as something given, but must investigate the laws according to which the morphogenetic processes concerned in its production operate. There is no doubt that the problem presented by the phenomena of morphogenesis is one of the most fundamental in biology. Just at present we are witnessing a period of remarkable activity in the investigation of the problems of heredity, and we are told that here lies the way to follow when in search of biological truth. No one can doubt either the immense importance of a determination of the laws of inheritance, or the value of the contributions to a knowledge of these laws which have been made during the last few years, both by the biometricians and by those working along Mendelian lines. Yet one ventures to think that it is of equal importance that our knowledge of the laws of morphogenesis be extended. In the zeal for the new thing represented by Mendelian inheritance and the phenomena of mutation there is a tendency to overlook the fundamental significance for our whole outlook on the broader problems of biology, of the results which

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have been obtained in the field of "Entwickelungsmechanik," and to forget that there is still a very great deal to be done in this field. Indeed, hardly more than a good start has been made towards the analysis of the factors concerned in form production.

It is the belief of the writer that in the methods of biometry we have an analytical tool capable of rendering great aid in the investigation of the problems of morphogenesis, and in just the direction where aid is most needed. Observation and experiment yield results which, whether they are quantitative or qualitative, certainly demand quantitative analysis if we are to get at their full meaning. In the physical sciences not only has the necessity for quantitative (i. e., mathematical) analysis of observational data long been recognized; but further, the greatest generalizations of those sciences have come as the result of such analysis. Unless one is prepared to maintain that the phenomena of the inorganic world are fundamentally different in kind from those in the organic, I can see no reason why a method of investigation which has proven so valuable in the physical sciences should not, with proper development, prove equally fruitful in the biological.

We may now consider briefly the precise nature of the present study. As has been stated above, our problem was to determine and formulate so far as possible the laws according to which differentiation with growth occurs in Ceratophyllum. If we take an individual Ceratophyllum plant, we find it to include a number of whorls of leaves all generally like each other but differing in detail. For example, some whorls have a larger, some a smaller number of leaves. A very little study suffices to show that whorls with different numbers of leaves distribute themselves about a typical condition in a characteristic way. Whorls with one particular number of leaves occur in a different proportion than do those with either more or fewer leaves. In this way, if we take into account all the whorls on the plant, we get a characteristic frequency distribution for the different numbers of leaves, such as is shown, for example, in fig. 5 (p. 25, *infra*). Further, as we shall see, the character of the frequency distribution is fundamentally the same, whatever may be the absolute size or source of the plant. Our problem is to determine so far as possible the biological factors that result in the production of this characteristic distribution. A whorl of leaves is the product of a definite morphogenetic process in the growing bud, and it seems not unreasonable to suppose that there is a definite set of factors (internal and external) which determine the number of leaves which each particular whorl shall bear. Moreover, we can be reasonably certain that since the nature of the distribution is the same for Ceratophyllum plants generally, some of these factors at least are constant in their action. Through

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them, in some way, it is determined that each definite kind of differentiated whorl shall occur among all whorls in a particular proportion. What are these constant factors and according to what laws do they operate? This is our problem.

We have, then, by analysis of the gross frequency distribution for the plant as a whole, to investigate the biological laws which lead to the production in this particular organism of the characteristic distribution observed. In biometrical terminology our problem is one of intra-individual variability.

Specifically it seemed very desirable to study in detail such questions as the following:

(1) The relation between the form of a given part and position in the organism as a whole. Does the number of leaves in a given whorl of a Ceratophyllum plant bear any definite relation to the position of that whorl? Such a relationship between position and differentiation has been found in a number of cases. (Cf. Pearson (:05), illustrations A and D; also Shull (:05) and Tammes (:03), for example.)

(2) The relation of such a positional differentiation to the variation and correlation of the differentiated parts. Does the variation exhibited among all the whorls occupying the same position on Ceratophyllum plants bear any definite relation to the position on the plant?

(3) The effect of environmental influences on positional differentiation.

(4) The effect of environmental influences on the growth of the organism as a whole.

(5) The relationship between intra-individual, intra-racial, and inter-racial variation and correlation.

These statements will suffice to indicate the general standpoint from which the work was done, and consequently it will not be necessary to enumerate further at this point the specific questions investigated.

Ceratophyllum is in many respects a very favorable form for the study of such problems as those outlined. It usually occurs in great abundance wherever it is found at all, and, being a widely distributed plant, can easily be obtained from a variety of habitats. Furthermore, the individual plant attains to a large size, which is very important for work on intra-individual variability. The plant is comparatively simple in structure and presents characters easily capable of quantitative determination. It would, in fact, be almost ideal for an investigation of this kind were it not for the fact that, as will be shown later in the paper, the differences produced in the form of the plant by different environments are not very marked. Ceratophyllum appears to be a much less plastic form than many of the land plants.

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At the time when the work was begun the writer had not yet seen the brilliant memoir by Professor Pearson on "Homotyposis in the vegetable kingdom" (Pearson, :01). When later this memoir had been read it was apparent that the problems which had been set for investigation in Ceratophyllum were fundamentally similar to those which Pearson had before him. There were, however, certain differences in standpoint which seemed to make it desirable to go on with this work. Pearson was concerned mainly with the determination in a wide series of forms of the amount of the homotypic correlation. To quote his own words (loc. cit., p. 294), the principle he was investigating was "the principle that homotypes are correlated, i. e., that the variation within the individual is less than that of the race, or that undifferentiated like organs have a certain degree of resemblance." From this standpoint he very naturally dealt, so far as possible, with undifferentiated or slightly differentiated like parts, not concerning himself at that time with any special investigation of the factors which produce differentiation in the repeated parts of plants. As will have been apparent from what has gone before, it is with this latter problem that the present work has to do. Our present aim is to examine as many as possible of the factors concerned in producing differentiation of homologous parts, and determine their effect on the intra-individual variability of the differentiated parts. For such a study it seems best for practical reasons to use at first only one organism, and make the investigation of that as thorough and as detailed as possible. It will thus be seen that this work, while not concerned with the determination of the degree of homotyposis in a particular plant, yet deals with one of the fundamental problems of homotyposis, and in so far may be considered supplementary to Pearson's memoir on that subject.

This work was begun early in 1902 by Miss Olive M. Pepper, at that time a student in the Zoological Laboratory of the University of Michigan. During the summer of 1902 Miss Pepper collected and nearly finished the counting of the plants in Series I, II, and III (cf. p. 13, *infra*). During the first half of the academic year 1902–03 she continued the work, sorting the data into frequency distributions and making some start on the computing. During this year she determined and recorded the data for Series IV. As it was impossible for Miss Pepper to go on further with the work, it was then carried forward as opportunity offered by the writer, by whom practically the whole of the raw material was reduced. When in the spring of 1905 it became possible, through a grant from the Carnegie Institution of Washington, to get some aid for the biometric work in hand, an assistant, Miss Florence J. Hagle, was

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put on this work. To her are due the determinations of the raw material of Series V and VI, and an independent verification of the computations for Series I, II, and III. The rest of the work and the arrangement of the material for publication is due to the writer.

To the Carnegie Institution I am greatly indebted for a grant in aid of this and other biometric work now in progress. Without this aid it would have been quite impossible to have brought the work to completion at this time. To Prof. Karl Pearson I am very grateful for valuable suggestions and advice, especially on the mathematical side of the work.

A word should be said regarding the arrangement of the paper. On account of the number of topics dealt with and the consequent length of the paper as a whole, it has seemed best to include a brief summary and discussion of the results of a particular section in that section itself rather than reserve all discussion for the end. This I believe will conduce to clearness.

MATERIAL AND METHODS.

The plant on which this work is based, *Ceratophyllum demersum*,[1] is a submerged aquatic which has a wide distribution. It is usually found in quiet rather than running water, and under favorable conditions forms great masses of vegetation. It commonly occurs in shallow water, frequently extending to the very edge of the pool where it is growing. The plant consists of a main axis, which may attain a length of 5 or 6 feet, from which spring a varying number of lateral branches. At more or less regular intervals along the main axis and the branches are whorls of leaves. These leaves are elongate and very narrow, being reduced practically to the form of rods. This shape of leaf is undoubtedly to be regarded as an adaptation to aquatic conditions. (Cf. Schenk, '86, and Henslow, '95.) At their outer ends the leaves divide, leading to the form of whorl shown in fig. 1. This division of the leaves at the outer end is the usual condition for Ceratophyllum. The plant has no root in the strict sense, but, as has been shown by the excellent physiological study of Pond (:05), probably absorbs all its nutrition directly from the water. It thus exhibits a practically perfect adaptation to aquatic conditions of existence. The lower end of the main axis of the plant is usually embedded for a distance of several inches in the layer of soft mud and plant débris which forms the substratum of a Ceratophyllum bed. This portion of the axis which is embedded is more or less etiolated and usually bears only the broken remnants of leaf-whorls. There

[1] I follow Pieters (:01) in designating the species of Ceratophyllum found about Ann Arbor *demersum*. I have not myself been able to get plants in flower.

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is absolutely no indication of root-hairs on this etiolated portion of the stem. At the ends of the branches and of the main axis of normal, healthy plants are found growing buds which at intervals form new whorls. At the tips of the branches the internodes become progressively shorter as we go towards the end, thus giving rise to the compact mass of leaves at the tip of the branch which is so characteristic of Ceratophyllum.

The plant is monœcious, both staminate and pistillate flowers being borne on the same individual. A detailed morphological study of the development of the flower has been published recently by Strasburger (:02). Reproduction is not entirely by seed, but a form of vegetative multiplication occurs very frequently (cf. Schenck, '86). At the approach of winter the tips of branches bearing growing buds break off and sink to the bottom. Since the bud is protected by the thickly matted leaves of the whorls near the tip it is able to winter over in this condition. With the advent of spring, growth begins again and by its continuance the bud gives rise to a new plant. In the early spring young plants which have been formed in this way may be found in various stages of growth. When the conditions are not too severe the plant as a whole winters over, renewing its growth in the spring like a perennial. This fact was first noted by Irmisch ('53, p. 528), who says regarding the "Dauer der Ceratophyllum-Arten:"

> Sie sind, wie ich mich überzeugt habe, bestimmt perennierend. Viele Examplare fand ich im Frühjahr an der Spitze der den Winter über frisch gebliebenen Zweige, die sich nicht weiter verändert hatten, weiterwachsen; in anderen Fällen waren die Blätter der Zweigspitzen bogig übereinander gekrümmt und die ältern Internodien des Zweiges waren abgestorben, so dass sie kleine lochere, isolirte Bollen darstellten. Auch diese wuchsen im Frühjahr weiter.

Certain of the plants (in Series V and VI) used in the present study were collected in the spring after having passed the winter in this way without dying or being broken up.

The characters of the plant with which the present study has principally to do are the following:

(1) The number of leaves in the whorl. For verbal convenience this character will be referred to throughout as "leaf-number."

(2) The position of the whorl on the plant, relative to the main axis.

(3) The size of the various divisions of the plant, as measured by the number of whorls they bear.

(4) The position of the branches, relative to the proximal end of the main axis.

With reference to the determination and recording of these characters the following should be said: The character "number of leaves to the whorl" was easily determined for the majority of the whorls, but

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became difficult near the ends of the branches. There the whorls are very small and closely packed together, and in order to make an accurate count it was necessary to use a lens, and in some cases even the compound microscope. For the sake of uniformity it was necessary to adopt some arbitrary rule with reference to divided leaves. After examining a considerable number it was decided to count *only the proximal ends of leaves.* Thus the whorl shown in fig. 1, would be recorded as having 8 leaves.

The number of leaves in every unbroken whorl on the plant was determined for each plant studied. In case a whorl was so mutilated as to make the determination of the number of leaves doubtful, it was so recorded. Unfortunately Ceratophyllum is rather liable to mutilation because of the fact that its tissues are brittle. In comparison with the total number of whorls on the plant, however, the number so mutilated as to be undeterminable was very small.

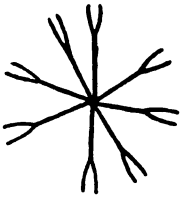

FIG. 1.—Diagram of a whorl, showing form of leaves.

In recording the position of the whorls the plan followed was to give each whorl on a particular portion of the plant a consecutive number, beginning with the proximal. In doing this the different axial divisions of the plant were treated separately. The first of these is the main axis, or, as it will be called throughout the paper, the "main stem." Using the usual notation for branching, we have designated the lateral branches arising from this main stem "primary branches;" those arising from primaries, "secondary branches;" those arising from secondaries, "tertiary branches," and so on. "Quaternary branches" were the highest lateral-branch elements found in any of our plants. Of these divisions the main stem alone presented any practical difficulty in making the records. It often happens in Ceratophyllum that the main stem branches dichotomously at a distance from its proximal end which varies in different cases. Are the two new axes to be considered as continuations of this stem, or is one to be regarded as a continuation of the main stem and the other as a large primary branch to be included in the records with the lateral branches? If the axes really arise by dichotomy of the main stem it is clear that they ought to be recorded as parts of it. The only difficulty is the practical one of being certain in a particular instance that we are not dealing with a case of unusually vigorous growth of a lateral branch which comes to rival the main stem in size. As a matter of fact it was found very early in the work that the first few whorls of lateral branches are so clearly differentiated that it is always possible in a given case of branching to tell whether

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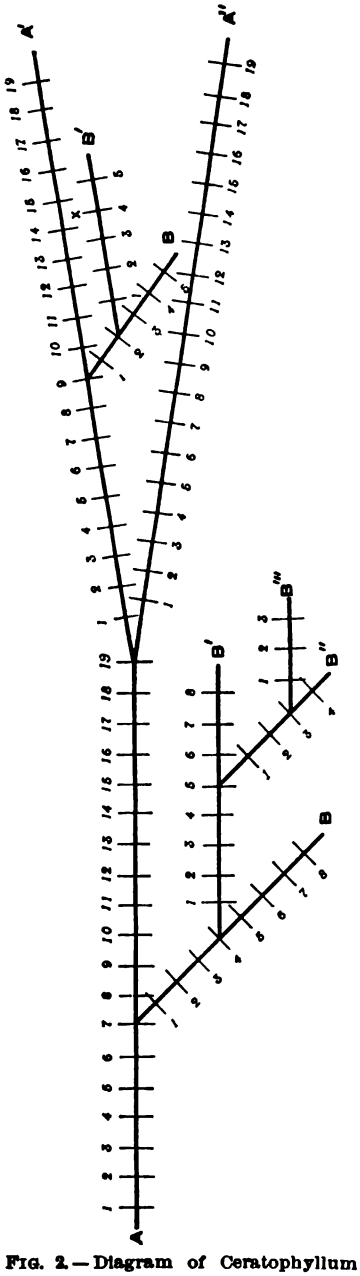

FIG. 2.—Diagram of Ceratophyllum plant, showing plan of making record. *A*, main stem; *A'*, *A''*, secondary main stem; *B*, *B*, primary branches; *B'*, *B'*, secondary branches; *B''*, tertiary branch; *B'''*, quaternary branch. The numbers indicate the manner in which position is recorded.

or not dichotomy of the main stem has occurred. Consequently each case of this kind was decided by a careful examination of the parts, and if it was found that each of the two axes possessed the characteristics of main stems they were recorded as "secondary main stems."

The whorls on each of these divisions of the plant (main stem, secondary main stem, primary branch, secondary branch, etc.) were numbered consecutively, beginning with the most proximal as 1. In this way the position of every whorl on the plant was recorded. These position records also gave the size, as measured by number of whorls borne, for each division of a plant. Furthermore, in recording a whorl from the axil of which one or more branches arose, a note was made of the origin of branches at that point.

The whole system of records will be made plainer by reference to a diagram of an imaginary Ceratophyllum plant. Such a diagram is given in fig. 2, in which the whorls are represented by short cross lines. It will, of course, be understood that in an actual plant the branching would usually be much richer than is indicated by the diagram. The diagram shows, however, that our records were such that we could reconstruct from them the entire plant as it existed. Thus the record on our data slips of a whorl like that marked with an x in the diagram would, when translated, signify that this whorl was the fourth whorl on a secondary branch from which no tertiaries arise and that this particular secondary branch sprung from the axil of the second whorl of a primary branch, which in turn arose at the ninth whorl of a secondary main stem beginning just beyond the 19th whorl of the original main stem. Since our records are of this kind for every

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plant studied, it will be seen that they give more complete data for the study of positional differentiation than probably has hitherto been available for any plant.

Our material came from three localities and is representative of four distinct habitats. It is comprised in six series, an account of which follows.

Series I, II, and III.—The plants composing these series were collected in the summer of 1902, from Carp Lake, near Grand Traverse Bay, in the northern part of Michigan. Carp Lake is a long and narrow body of water extending about 18 miles in a generally north and south direction, with an outlet into Lake Michigan at its northern end. At its narrowest part it is only about a half mile in width. At this point there is a neck of marshy land extending out into the lake from the east side and reaching more than halfway across it. On the north side of this strip of land (known locally as Fountain Point), the plants of Series I, II, and III were collected. They all came from a small open space surrounded by an abundant growth of cat-tails and reeds (Juncus sp.). The situation in which Ceratophyllum was growing was well protected from the wind, and consequently the water about the plants was rarely much disturbed. The plants were directly exposed to the sunlight, there being no overhanging trees or bushes. The bottom was similar to that usually found under Ceratophyllum beds. The proximal ends of the plants were buried in soft, loose, black mud, containing much decayed plant débris, which came mostly from the Ceratophyllum itself. The growth of the plant at this place was very abundant. The individual plants were so matted together in the main mass composing the bed that it was only with difficulty that a single one could be disentangled unbroken.

The dates of collection for the three series were as follows:

Series I: Collected July 22, 1902. At this time the water at the point of collection was 2 feet deep.

Series II: Collected August 18, 1902. Water at point of collection approximately 15 inches deep. The level of the whole lake had lowered since the first collection. The water surrounding the plants was very muddy.

Series III: Collected August 25, 1902. Conditions were the same as when the Series II collection was made.

Series I included 5 plants, Series II, 2 plants, and Series III, 1 plant. The reason why Series II and III did not include larger numbers was the great difficulty of collecting unbroken specimens after the water had become so low. The matting together of the plants in the bed was so close as a result of this lowering that to disentangle a large plant

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without breaking off many of its branches was practically impossible. We had, then, to be content with few specimens. The individuals in these series were fairly large, and considering the dates of collection may be taken as representative of the "adult" condition of the plant. In other words, it is not probable that if these plants had been left undisturbed much further growth would have taken place that year.

To sum up: Series I, II, and III, include 8 complete Ceratophyllum plants, coming from quiet water near the shore of Carp Lake in northern Michigan. These plants were collected in mid-summer, the three collections covering a period of time of approximately one month, and may be considered to represent the condition at the height of the growing season.

Series IV.—This series was collected at Ann Arbor, Michigan, on October 15, 1902. The plants were taken from a very extensive and flourishing bed of Ceratophyllum which grew at that time[1] near shore in the shallow back-water below the dam across the Huron River. The water was comparatively quiet, but there was always a slow current, which after heavy rains became rapid. So far as this factor in the environment is concerned the Series IV plants represent distinctly different conditions than do those of Series I, II, and III. The character of the bottom was also somewhat different. In the river habitat there was very little of the mass of plant débris which in ponds and lakes accumulates under Ceratophyllum beds. Apparently a considerable part of this material was carried away by the current in the river. The plants were attached; that is, the proximal ends were embedded in the soft mud of the bottom. The water at the point where the collection was made was approximately 18 inches deep. The bed was shaded by overhanging trees and bushes on its east side, but was fully exposed on its west side. As will be noted, the collection was made late in the season, so that the plants may be regarded as certainly full grown.

The series includes two plants. One of these was a very large one, bearing over 900 whorls and over 100 branches. In some respects this was the most satisfactory series of all. There were comparatively few broken whorls and the large size of the individuals gave an excellent collection of data.

Series V and VI.—The plants in these series all came from a small pond formed as a cut-off of the Huron River. It is situated some 3½ miles below Ann Arbor, just west of the upper end of the Geddes millpond. The pond still retains its connection with the river through a

[1]Later this bed was completely washed away by the breaking of a dam in a spring freshet.

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narrow (6 to 8 feet) channel. It lies on the south side of the river. The bottom of this pond is covered with a dense mass of aquatic vegetation, principally consisting of Chara, but with a good deal of Ceratophyllum about the edges of the Chara banks. On the north side of this pond, which is about a hundred yards wide, there is a thick growth of willows and alders, which overhang the edge and give a considerable amount of shade to the Ceratophyllum beneath. On the south side, on the contrary, there is no shade whatever, the aquatic plants being exposed to the full glare of the sun during the whole day. On the south side the Ceratophyllum was closely associated with Chara, forming a fringe about the Chara bed. On the north side, however, the Ceratophyllum was growing alone. In other respects the conditions were the same on the two sides of the pond. Series V, including 7 plants, was collected from the north side of this pond, and Series VI, including 6 plants, from the south side. The date of collection was May 21, 1905. The plants thus represent the early spring conditions. Nearly all the plants were small. The water where the different plants were taken varied between 6 inches and 2 feet in depth. The bottom was physically very like what has been described above for the Carp Lake habitat—soft black mud, with much plant débris. All the plants were attached. The water is very quiet, as the pond is well protected from the wind, and there is no appreciable current. The plants of these two series were of special interest because of the fact that they included representatives of each of the methods of passing the winter which have been mentioned above (p. 10). Plants 1, 2, 6, and 7 of Series V, and plants 1, 2, 4, 5, and 6 of Series VI had wintered over unbroken and had begun new growth in the spring without having lost their individuality of the previous year. The other plants of these two series had started in the early spring, either from seeds or from separated winter buds.

Putting all the series together, it will be seen that we have plants from the beginning, the height, and the end of the growing season, representing lake, pond, and river habitats. Our material must, then, be regarded as fairly comprehensive.

Finally, a word may be said regarding the calculations. I have followed throughout the plan of calculating the standard deviation from the *unmodified* second moment, wherever it was to be used simply as an index of variation. In calculating the moments for fitting curves to the observations I have tried Sheppard's corrections wherever there was any approach to high contact at the ends of the range, but usually with not very satisfactory results (cf. p. 23, *infra*). In each case a statement is made as to whether the moments were modified or not.

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VARIATION IN CERATOPHYLLUM—GENERAL RESULTS.

Before analyzing our material in detail it is desirable for purposes of orientation to examine in a general way the nature and amount of the variation exhibited by the plant. To this end the present section is devoted.

In this section I shall only consider the variation in the number of leaves to the whorl, when all the unmutilated whorls on the plant are taken together without reference to their position, leaving until later other characters studied. The frequency distributions for this character for each plant separately and for each series are given in table 1.

We see at once from this table that the range of variation in leaf-number is rather limited in Ceratophyllum. Whorls with 4 leaves and whorls with 11 leaves include practically the whole of the variation in this character, though whorls with 12 and 3 leaves do occur very rarely. The great bulk of the whorls have either 8, 9, or 10 leaves. Considering the first four series, it is seen that whorls with 9 leaves occur more frequently than do any other single class, thus making 9 the observation mode. From mere inspection of the frequency distributions it is quite clear that while Series I, II, III, and IV are all very closely alike in respect to the character under consideration, on the other hand the two series taken at the beginning of the growing season (V and VI) are in some respects quite different. The plants of these latter series are generally small, and the distributions are irregular. The reason for this irregularity will be discussed later, but for the present it needs merely to be kept in mind that the distributions of Series V and VI represent the action of special factors which do not influence the other series.

In order to bring more vividly to the reader's mind the nature of the variation in this character, the diagrams shown in fig. 3 have been prepared. These give frequency polygons for the totals of each of the series (distributions No. 44, 61, 62, 97, 139, and 176). These are so plotted as to have equal areas; that is, the frequencies are reduced for each series to percentages and then plotted to the same base unit.

From these diagrams the essential similarity in the frequency distributions for Series I, II, III, and IV comes out in a very striking way. Series IV shows a higher frequency of whorls with 9 leaves and a lower frequency of those with 6 leaves than do Series I, II, and III, but otherwise differs very little from these. All the distributions show a marked degree of asymmetry about the mode. The range below 9 whorls is roughly twice as great as the range above that number. One point to which I wish to call attention here, as it is shown very clearly by the

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diagrams, is that if we compare Series I, II, and III with each other it is noticeable that, of the three, Series I has the lowest frequency of whorls with 10 leaves, Series II has about 2 per cent more 10-leaved

TABLE 1.—*Frequency distribution for variation in number of leaves per whorl for all unmutilated whorls, without reference to position on the plant.*

Series.	Plant.	Distribution number.[a]	Leaves per whorl.										
			3	4	5	6	7	8	9	10	11	12	Total.
I	1	1	...	...	1	12	25	45	65	78	2	...	228
	2	2	...	...	1	11	18	32	56	38	4	1	161
	3	3	...	...	1	17	17	38	56	31	3	1	164
	4	4	...	...	...	17	35	71	77	58	5	...	263
	5	5	...	...	...	4	4	16	22	13	2	...	61
	All plants..	44	...	...	3	61	99	202	276	218	16	2	877
II	1	45	...	...	2	48	72	126	191	161	15	...	615
	2	46	...	...	1	16	37	66	96	87	10	...	313
	All plants..	61	...	...	3	64	109	192	287	248	25	...	928
III...	1	62	...	...	...	44	50	101	170	151	7	...	523
IV	1	73	...	...	...	3	54	140	228	182	3	...	620
	2	74	1	0	1	16	118	196	326	261	3	...	922
	All plants..	97	1	0	1	19	172	336	554	443	6	...	1,532
V	1	98	...	4	30	30	85	68	93	72	3	...	385
	2	99	...	...	...	...	2	2	2	2	...	...	8
	3	100	...	...	...	...	1	7	5	9	...	...	22
	4	101	...	...	...	...	2	5	6	...	...	...	13
	5	102	...	...	...	...	6	7	6	5	...	...	24
	6	103	...	...	...	4	6	10	25	16	...	...	61
	7	104	...	...	1	12	34	33	50	16	1	...	147
	All plants..	139	...	4	31	46	136	132	187	120	4	...	660
VI	1	140	...	...	...	7	7	15	27	23	...	...	79
	2	141	...	...	3	4	15	23	20	11	...	...	76
	3	142	...	...	1	5	5	10	15	8	2	...	46
	4	143	...	...	...	3	12	11	9	5	1	...	41
	5	144	..	...	5	6	26	45	60	74	...	...	216
	6	145	...	...	2	2	13	30	43	130	15	1	236
	All plants..	176	...	...	11	27	78	134	174	251	18	1	694
I, II, III	All plants..	177	...	...	6	169	258	495	733	617	48	2	2,328

[a] The "distribution numbers" are merely the serial numbers by which the distributions are designated in our notes. They have been retained in the paper for convenience in referring to particular distributions.

whorls, while Series III has 4 per cent more of such whorls than does Series I. In other words, there is a progressive increase in the proportion of 10-leaved whorls as we go from Series I to Series III. The

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explanation of this fact will be taken up later when certain other results are in hand. In anticipation of these results it may be said that the matter is related to the fact that Series II and III were collected at later dates than Series I, and the change is a growth phenomenon.

Examining the frequency polygons for Series V and VI, we see that these are essentially different both from each other and from all the other series. Series V, while it has as the most frequent whorls those

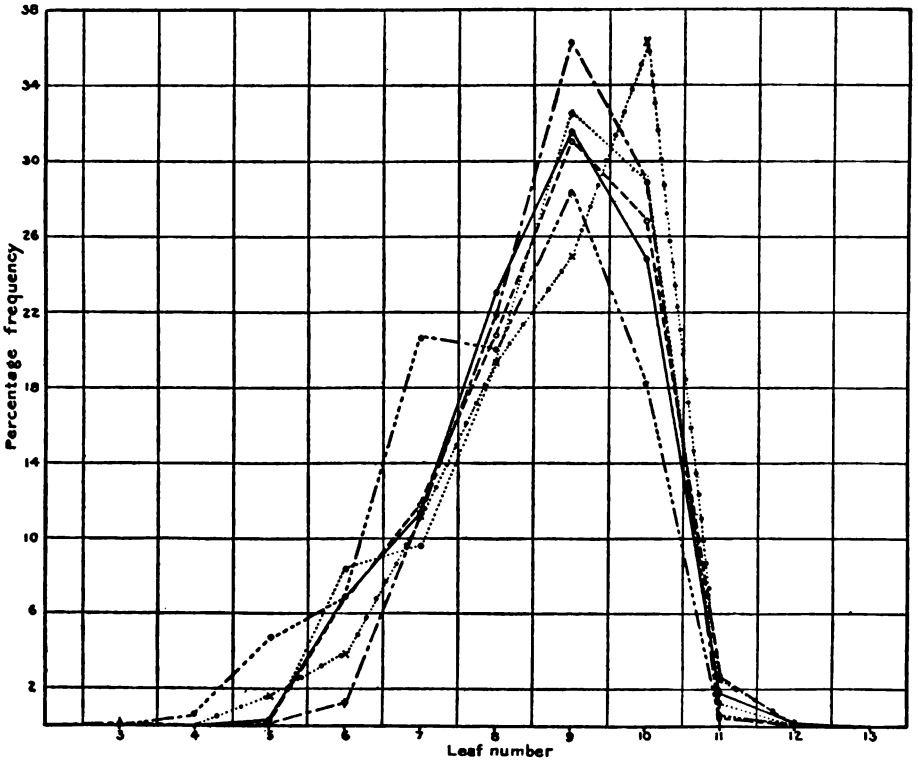

FIG. 3.—Frequency polygons for variation in leaf number. Totals for series. The abscissæ give the number of leaves per whorl and the ordinates frequencies per cent. Series I, ●———— ; Series II, o- - - - - - ; Series III, ●····· ; Series IV ♦——·—·; Series V, o- - - - — ; Series VI, x·o···o···o.

with 9 leaves, yet differs from the other series in having a comparatively high frequency of whorls with 7 leaves. The polygon for Series VI is quite smooth and regular, yet differs from all the others in having, as the most frequent class, 10-leaved whorls.

With these polygons before us the nature of our task becomes perhaps plainer. We find that when we determine the number of leaves in every whorl of each plant and plot up the results we get these very

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smooth and regular polygons. But these polygons represent composites. While they show the condition of the plants as a whole with respect to variation, they tell us nothing about how this condition comes to be. Our purpose is to analyze, piece by piece, these gross frequency polygons and try to find out the different factors which determine the proportionate frequencies of whorls of different types. In other words, we must by statistical analysis *dissect* these polygons, and in that way, if possible, gain some idea of the physiological factors to which they fundamentally owe their origin. By proceeding in this way it should be possible to obtain results of real significance.

In the continuation of our preliminary survey we may next examine the values of the chief physical constants, means, standard deviations, and coefficients of variation of the distributions given in table 1. These constants are collected in table 2.

This table brings out a number of points of interest. In the first place, we note again that in respect to all the constants Series I, II, and III are very much alike, whether we compare the series as wholes or take single plants. Series IV is significantly but not widely different from Series I, II, and III. It has a somewhat higher mean number of leaves to the whorl, and a lower variability in this character. Series V differs from the others in having a lower mean and higher variability.

If, in order to get a general idea of the values of the constants for variation in the Ceratophyllum of this region, we take the means of the constants for the six series, weighting them in each case with the number of whorls they include, we have the following results:

Mean of means	8.655
Mean of standard deviations	1.206
Mean of coefficients of variation	13.966

It may, then, be fairly concluded that the Ceratophyllum of this region has an average number of leaves to the whorl of about 8.7, a standard deviation of about 1⅛ leaves, and a relative variability of approximately 14 per cent.

It is of some interest to compare these results with the statements of botanists who have investigated Ceratophyllum from other standpoints. The first thoroughly scientific investigation of the biology of Ceratophyllum was that of Schleiden ('37). Considering its date this memoir is a most remarkable one, both for the wealth and the accuracy of its observations. Regarding the number of leaves to the whorl Schleiden says (loc. cit., p. 516): "Der Stengel der Pflanze ist stielrund mit vollständigen Knoten versehen, an denen sich die Blätter in 6–10 theiligen Wirteln befinden. Smith giebt fälschlich 8 als Regel (cf. Eng-

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lish Flora, I)." From this one must conclude that Schleiden either did not count any considerable number of whorls, or else that he was dealing with a highly differentiated local race. Judged by our data "Smith" did not come far from the "Regel" by placing it at 8. Klercker ('85), in his frequently quoted paper on the anatomy and embryology of

TABLE 2.—*Constants of variation in number of leaves per whorl for all unmutilated whorls, without reference to position on the plant.*

Series.	Plant.	Distribution number.	Mean (unit—1 leaf).	Standard deviation (unit—1 leaf).	Coefficient of variation.
I	1	1	8.768±0.054	1.208±0.038	13.777±0.443
	2	2	8.652± .068	1.277± .048	14.759± .567
	3	3	8.470± .069	1.309± .049	15.451± .589
	4	4	8.529± .050	1.208± .036	14.160± .425
	5	5	8.689± .101	1.167± .071	13.432± .835
	All plants	44	8.613± .027	1.201± .019	13.938± .229
II	1	45	8.624± .035	1.283± .025	14.876± .292
	2	46	8.728± .047	1.236± .033	14.157± .389
	All plants	61	8.659± .028	1.268± .020	14.645± .234
III	1	62	8.679± .037	1.254± .026	14.446± .307
IV	1	73	8.887± .026	.966± .019	10.870± .212
	2	74	8.758± .024	1.084± .017	12.375± .197
	All plants	97	8.809± .018	1.040± .013	11.810± .146
V*	1	98	7.987± .054	1.568± .038	19.636± .495
	7	104	8.063± .067	1.195± .047	14.644± .588
	All plants	139	8.155± .038	1.430± .027	17.540± .480
VI	1	140	8.658± .093	1.231± .066	14.221± .778
	2	141	8.132± .097	1.260± .069	15.497± .868
	3	142	8.413± .140	1.408± .099	16.732±1.209
	4	143	8.098± .129	1.226± .091	15.138±1.153
	5	144	8.718± .058	1.254± .041	14.387± .476
	6	145	9.394± .049	1.117± .035	11.888± .374
	All plants	176	8.820± .032	1.243± .022	14.091± .260

*In Series V the constants for the very small plants (plants 2, 3, 4, 5, and 6) are not separately tabulated.

Ceratophyllum, has the following to say regarding the number of leaves in the whorl (loc. cit., p. 8): "Le nombre [i. e., of leaves] dans chaque verticelle en est en general constant sur le même axe, mais varie avec les axes. J'en ai trouve 7–12." This range agrees fairly well with what we have found, though starting higher. It is in all probability, however, a general estimate rather than the result of any extensive counting.

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Schenk ('86), in his well-known "Biologie der Wassergewaechse," gives the number of leaves to the whorl as between 6 and 10, but no special weight is to be given to this statement, as it is clear from internal evidence that his account of Ceratophyllum is very largely taken directly from Schleiden. Strasburger (:02), in his recent memoir on Ceratophyllum, says (p. 486), regarding the number of leaves to the whorl: "In den mir zur Verjügung stehenden Exemplaren von *Ceratophyllum submersum* war die Zahl der Blätter in den Quirlen sehr häufig zehn." Further references to the literature regarding this matter are unnecessary. The point I wish to bring out is merely that so far as we can judge from such very slender evidence, the condition of Ceratophyllum with respect to number of leaves in the whorl in European countries (Germany and Sweden) is apparently not very widely different from what it is in America.

TABLE 3.—*Coefficients of variation in plants.*

Authority.	Plant.	Character.	Coefficient of variation
Pearson (:03)	Ficaria ranunculoides	Number of sepals	3.24 to 22.02
Do	do	Number of petals	5.34 to 14.69
Do	do	Number of stamens	12.12 to 18.77
Do	do	Number of pistils	22.32 to 27.89
Shull (:02 and :04)	Aster prenanthoides	Number of bracts	11.62 to 27.00
Do	do	Number of rays	11.43 to 27.49
Do	do	Number of disk florets	9.66 to 27.41
Shull (:05*a*)	Onagra lamarckiana	Number of branches	15.7
Do	Onagra rubrinervis	do	15.0
Do	Onagra lamarckiana	Length of leaf	13.60
Do	Onagra rubrinervis	do	12.62
Pearson (:05)	Asperula odorata	Branches per whorl	18.49
Do	Equisetum arvense	do	45.48

The relative degree of variation in this character of Ceratophyllum as indicated by a coefficient of variation of about 14 per cent is of the same order of magnitude as that which Pearson (:01) has found for a variety of characters in different plants. In his table XXXIV (loc. cit., p. 361) are given the coefficients of variation for 26 cases, covering a wide range of plant forms and characters. These coefficients of variation range between 7.80 and 41.96, with a mean of 19.97. Our value for Ceratophyllum leaves comes very close to the coefficient measuring variation in the stigmatic bands of Shirley poppies, for example, or to that for the veins in the leaves of Spanish chestnuts. In order that a comparison may be made between other well-known biometric results on variation in plants and what we have found for Ceratophyllum, a table of coefficients of variation (table 3) has been prepared.

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It is apparent from inspection of fig. 3, or of the frequency distributions in table 1, that the variation in Ceratophyllum in respect to leaf-number is very skew. In order to bring out more precisely the amount of this skewness, as well as other important facts regarding the nature of the distributions, I have analyzed a portion of the data by the methods given by Pearson, in his fundamental memoir on "Skew Variation" (Pearson, '95) and its supplement (:01). I have dealt in this way with two of the distributions made up of all the whorls on each plant. The first of these distributions (No. 177, table 1) is that resulting if Series I, II, and III are combined, that is, it is what is obtained by adding together distributions 44, 61, and 62. It represents the variation of the character under consideration in the Carp Lake population of Ceratophyllum, taken as a whole. As has been pointed out in the preceding section, all the Carp Lake plants came from the same spot, and only differed in the time of collection. It is clearly evident from the diagrams in fig. 3 and the constants in table 2 that these three collections do not differ from each other significantly. The differences between the constants for the totals of these three series, as given in table 2, are small in comparison with their probable errors, which are themselves small, as we are dealing with relatively large numbers. Hence the series may be considered as three random samples of a homogeneous population and may be combined if it is desirable in order to bring out a particular point. The other distribution, which I have graduated for comparison with this, is that of plant 2, Series IV (No. 74, table 1). This plant was the largest single plant in our collections and for that reason was chosen for analysis. Others would have given essentially the same results, but with larger probable errors.

The problem of how best to treat analytically distributions of the sort given by Ceratophyllum is, as has been emphasized by Pearson (:01, p. 456), a very difficult one. We have, in the first place, in these distributions discrete variation, the observations proceeding by unit steps, while the mathematical function which we take to represent them is continuous; further, the distributions are markedly skew; the range is very small, giving less than ten observations to determine the moments from; and finally there is no approach to high contact at one end of the range. Hence, the determination of the true moments is by no means a simple matter. Proper corrective terms for use in such cases have not yet been worked out. Sheppard's corrections are theoretically not applicable. In the present instance by actual trial I obtained much worse results with Sheppard's corrections than with the raw moments, and consequently for lack of anything better the latter have been used in graduating these two distributions.

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The chief constants, both physical and algebraical, of the distributions are given in table 4. The unit is 1 leaf.

TABLE 4.—*Analytical constants for variation in leaf-number.*

Constant.	Series I, II, and III combined (Distribution No. 177).	Plant 2 of Series IV (Distribution No. 74).	Constant.	Series I, II, and III combined (Distribution No. 177.)	Plant 2 of Series IV. (Distribution No. 74)
Total frequency	2328	922	Skewness	—0.6332	—0.4432
μ_2	1.5888	1.1747	Modal divergence	— .7961	— .4804
μ_3	—1.0503	— .8331	Standard deviation	1.2573	1.0838
μ_4	6.5040	4.4627	Mean	8.6465	8.7581
β_1	.2793	.4281	Mode	9.4425	9.2385
$\sqrt{\beta_1}$	.5285	.6543	Modal frequency	704.58	344.90
β_2	2.6028	3.2341	Range	6.5028	9.8186
β_2-3	— .3972	.2341	Lower end of range	4.2547	1.1408
κ_1	—1.6323	— .8163	Upper end of range	10.7575	10.9594

The fact that the criterion κ_1 $(= 2\beta_2 - 3\beta_1 - 6)$ is in both cases negative indicates that curves of Type I are demanded. The equations to the curves for the two distributions are as follows:

Series I, II, and III:

$$y = 704.5833 \left(1 + \frac{x}{5.1878}\right)^{2.2857} \left(1 - \frac{x}{1.3150}\right)^{.5794}$$

Series IV, plant 2:

$$y = 344.8980 \left(1 + \frac{x}{8.0978}\right)^{9.2983} \left(1 - \frac{x}{1.7209}\right)^{1.9760}$$

The histograms and their fitted curves are shown in figs. 4 and 5.

From both the constants of table 4 and the curves themselves it is clear that the distributions deviate very far from normality. There is no doubt that both the kurtosis (cf. Pearson, :05) and the asymmetry of the curves are significant. In both cases the skewness is negative, the mode lying above the mean. The amount of the modal divergence is considerably greater in the case of the first curve (Series I, II, and III combined) amounting there to more than three-fourths of a leaf. Since frequency curves of Type I are of limited range, we have given for these two curves the theoretical range of variation. It is of interest to compare this with the observed range. In the Carp Lake race the observed range is between 5 and 12 leaves, inclusive. The theoretical range is between 4.25 and 10.76 leaves, a total of 6.51, as against the observed 7. Thus the total theoretical range is only about a half leaf different from

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the observed. It is not, however, distributed on the two sides of the mode in the same manner. The theoretical range overestimates the observed below and underestimates it above the mode. Thus the two whorls with 12 leaves are theoretically excluded. It is altogether probable that with proper corrective terms for the moments we should get a still better estimate of the range. In the case of plant 2, Series IV, the observed range is between 3 and 11 leaves, inclusive, or a total of 8. The theoretical curve has a range between 1.14 and 10.96, or a total of 9.82 leaves. No better result could be desired for the upper end, but

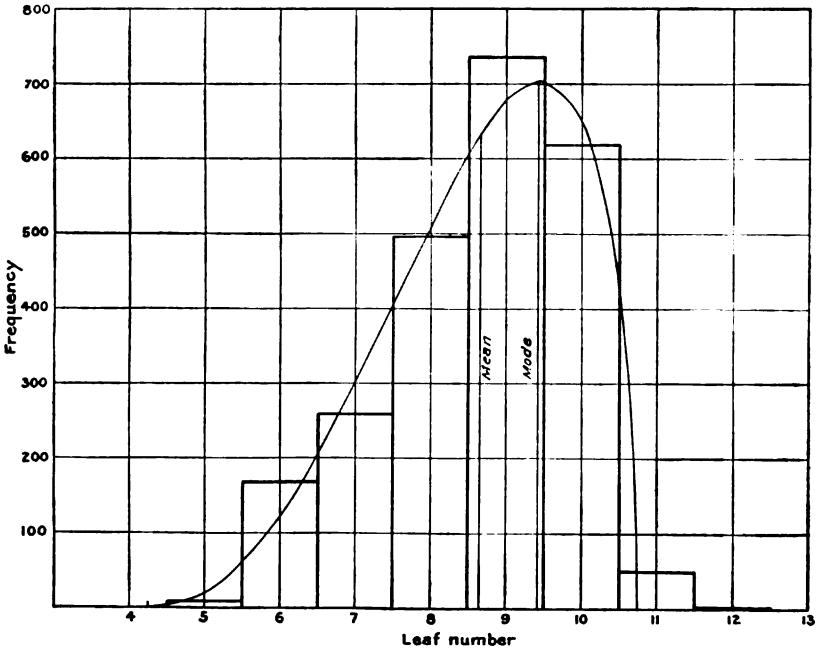

FIG. 4—Frequency histogram and fitted curve for variation in Ceratophyllum. All unmutilated whorls on all plants of Series I, II, and III.

the lower end is considerably overestimated. Thus, the occurrence of 2-leaved whorls is theoretically possible. There are three things which should be kept in mind, however, in passing judgment on this result. In the first place, the undue extension of the lower end of the theoretical curve is in a large measure due to the single observation of a 3-leaved whorl. Now, this whorl was almost certainly to be regarded as an abnormality. It was a very small whorl in respect to size as well as number of leaves. It presented the appearance, to borrow zoological terminology, of being an intercalated, abnormal whorl between two normal ones. What its origin was it is impossible to say, but it cer-

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tainly presented the appearance of being a teratological formation. In the second place, it should be noted that while the end of the range is theoretically at 1.14, the proportionate frequencies as given by the curve for ordinates below that at 4.5 are excessively minute. Thus the absolute frequency according to the theoretical curve for whorls of two leaves is 0.00004.[1] Or, in other words, the expectation of whorls with

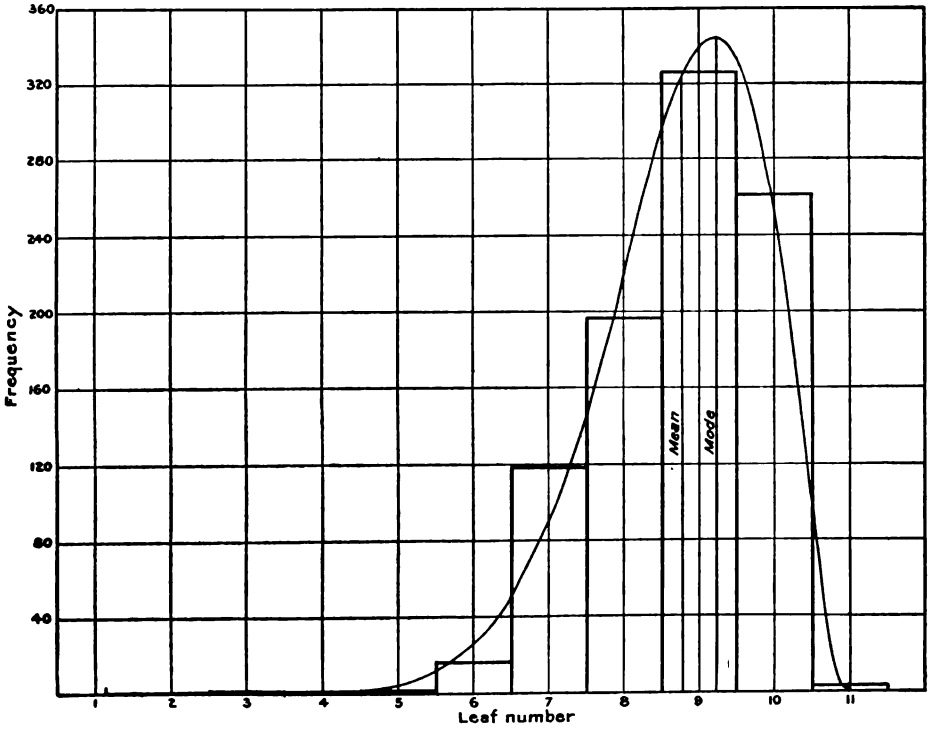

FIG. 5.—Frequency histogram and fitted curve for variation in leaf-number in Ceratophyllum. All unmutilated whorls on plant 2, Series IV.

two leaves given by the theoretical curve is that there will be 5 such whorls in every 100,000,000! Finally, we must remember that the range is subject to a very large probable error, both in respect to its absolute

[1] This is of course the *area* included in the range between 1.5 and 2.5, of which the mid-ordinate is at 2, and not the ordinate at 2. To pass from ordinates to areas the following formula, given by Pearson (:04) for a curve of Type I was used.

On strip of base h:

$$\text{Area} = h \times y \left[1 + \frac{h^2}{24} \frac{(m_1 + m_2)\,(x^2\,(m_1 + m_2 - 1) - a_1 a_2)}{d_1^2 d_2^2}\right],$$

where h is the base element having y as its mid-ordinate at a distance x from the mode, and d_1 and d_2 are the distances of y from the ends of the range.

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size and to its position. This is perhaps the most important point of all, and it is one which is usually overlooked in criticisms of Type I curves in regard to the estimation of the range.

On the whole, I think we may conclude that the curves give good fits and lead to entirely reasonable values for the physical constants.

A point of interest brought out by these curves is the very close similarity between the results for the combined Carp Lake plants, which may be considered representative of the local race, and the single plant. The curves are of very similar form, and the values of the constants are of the same order.

SUMMARY.

In this section the general facts regarding variation in the number of leaves to the whorl in Ceratophyllum have been brought out. It has been shown (1) that the observed range of variation in this character is from 3 leaves to 12 leaves, inclusive; (2) that the average number of leaves to the whorl is about 8.7, with a standard deviation of about 1.2 leaves, leading to a coefficient of variability of about 14 per cent; (3) that the variation is markedly skew in the negative direction, the modal whorl having a higher number of leaves (about 9.3) than the mean whorl; (4) that there are but comparatively small differences in respect to this character between series collected at different times and places; (5) that we reach essentially the same conclusions with reference to these general facts of variation, whether we take a single large plant or a number of plants from the same locality.

We have seen in this section, in a birdseye view, the facts presented by the plants when we study the individual as a whole, taking into account every whorl on the plant. The attempt may now be made to analyze these facts.

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VARIATION IN DIFFERENT PORTIONS OF THE PLANT.

In this section of the paper the material will be treated according to the following scheme:

Variation in whorls on the main stem.
Variation in whorls on primary branches.
Variation in whorls on secondary branches.
Variation in whorls on tertiary and quaternary branches.
Relative size of the different divisions of the plant and variation in this character.

It will be understood throughout that when the whorls on a particular division of the plant are referred to, all unmutilated whorls on that division are included.

TABLE 5.—*Frequency distributions for variation in leaf-number in main-stem whorls.*

Series.	Plant.	Distribution number.	Leaves per whorl.								
			5	6	7	8	9	10	11	12	Total.
I	1	178	...	1	1	5	19	43	1	...	70
	2	7	...	...	1	3	5	3	...	1	13
	3	179	...	1	4	8	16	19	1	1	50
	4	9	...	....	...	...	12	16	4	...	32
	5	10	...	3	1	2	5	3	1	...	15
	All plants..	24	...	5	7	18	57	84	7	2	180
II	1	47	...	...	1	2	13	35	12	...	63
	2	48	...	...	...	3	16	19	4	...	42
	All plants..	49	...	...	1	5	29	54	16	...	105
III...	1	67	...	...	1	3	22	57	6	...	89
IV	1	180	...	...	...	4	6	22	...	...	32
	2	181	...	...	1	3	17	29	...	...	50
	All plants..	82	...	...	1	7	23	51	..	...	82
V	1	105	3	2	9	8	11	13	1	...	47
	2	106	...	...	1	2	2	2	...	...	7
	3	107	...	...	...	1	2	7	...	...	10
	4	108	...	...	...	2	2	...	...	...	4
	5	109	...	...	1	1	5	5	...	...	12
	6	110	...	2	2	2	2	6	...	...	14
	7	111	...	...	3	3	18	5	1	...	30
	All plants..	112	3	4	16	19	42	38	2	...	124
VI	1	146	...	2	...	1	3	1	...	...	7
	2	147	1	...	5	8	12	8	...	...	34
	3	148	1	...	...	3	5	6	1	...	16
	4	149	...	2	5	3	4	3	1	...	18
	5	150	...	...	1	5	13	22	...	...	41
	6	151	...	...	...	3	10	21	7	...	41
	All plants..	152	2	4	11	23	47	61	9	...	157
I,II,III	All plants.....	180	...	5	9	26	108	195	29	2	374

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VARIATION IN WHORLS ON THE MAIN STEM.

The frequency distributions for main-stem whorls of the different plants and series are shown in table 5 (page 27). In this table all the divisions of the main stem are combined.

In order to bring out more clearly the form of these distributions, and to facilitate comparison, the frequency polygons for the totals of each of the six series have been plotted and are shown in fig. 6. All of

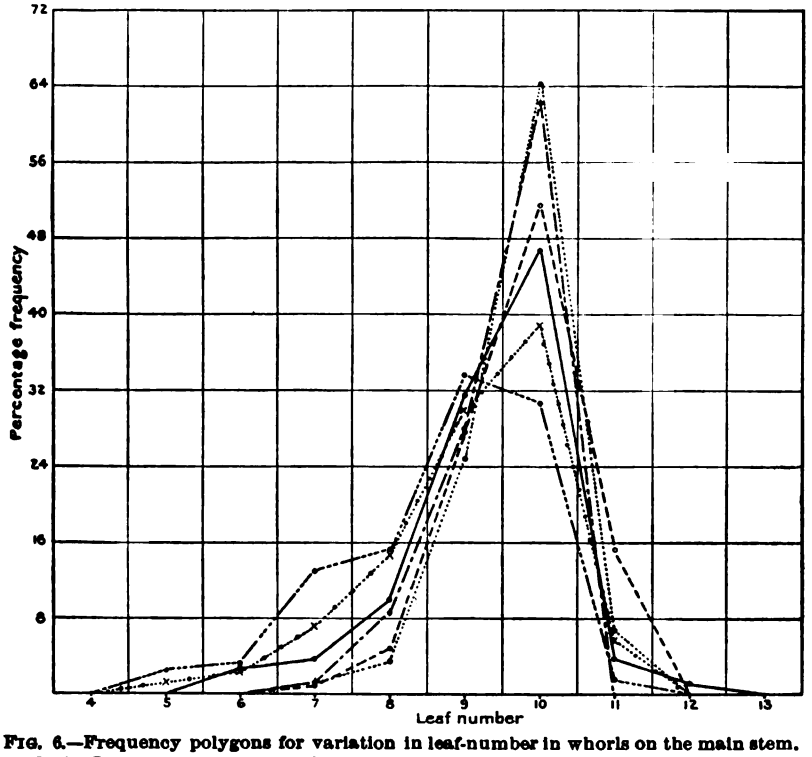

FIG. 6.—Frequency polygons for variation in leaf-number in whorls on the main stem. Series I, ●———— ; Series II, o- - - - - - ; Series III, ●····· ; Series IV, ◆——·——; Series V, ●- - - - —— ; Series VI, x-o····o····o. The ordinates give percentage frequencies.

these polygons are so plotted as to have the same area. The scale of the drawing is approximately the same as that of fig. 3 (p. 18) so that direct comparisons may be made.

From the distributions and polygons it is seen that on the main stem the most frequently occurring whorls are generally those having 10 leaves. Series V is the only exception to the rule, and in that case whorls with 9 or 10 leaves are within the error from random sampling equally frequent. There is distinctly less "scatter" in the main-stem

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as compared with the "total" polygons given in fig. 3, indicating, of course, that main-stem whorls are less variable. A more precise notion of the variablity of the whorls on this portion of the plant may be gained from table 6, which gives the means, standard deviations, and coefficients of variation for the larger of the main-stem distributions.

TABLE 6.—*Constants for variation in leaf-number in main-stem whorls.*

Series.	Plant.[a]	Distribution number.	Mean (unit = 1 leaf).	Standard deviation (unit=1 leaf).	Coefficient of variation.
I	1....	178	9.500±0.066	0.824±0.047	8.671±0.486
	3.....	179	9.480± .099	1.084± .070	10.909± .743
	All plants..	24	9.317± .053	1.062± .038	11.397± .410
II	1.....	47	9.873± .069	.807± .048	8.169± .494
	2.....	48	9.571± .079	.760± .056	7.945± .588
	All plants..	49	9.752± .053	.802± .037	8.225± .385
III...	1.....	67	9.719± .049	.687± .035	7.066± .359
IV...	All plants.....	82	9.512± .074	.703± .037	7.387± .391
V	1.....	105	8.383± .150	1.524± .106	18.175±1.305
	7.....	111	8.933± .110	.892± .078	9.984± .878
	All plants..	112	8.734± .078	1.283± .055	14.694± .643
VI	2.....	147	8.588± .135	1.166± .095	13.578±1.130
	5.....	150	9.366± .083	.789± .059	8.422± .632
	6.....	151	9.780± .086	.812± .060	8.301± .623
	All plants..	152	9.089± .065	1.212± .046	13.338± .517

[a] The constants were not separately calculated for plants in which there were only a few main-stem whorls.

On account of the small number of the main-stem whorls the results are not as regular as could be desired. Even in very large Ceratophyllum plants there are usually a comparatively small number of main-stem whorls, and of those originally present a part are usually so mutilated as to be uncountable. As the main stem is the oldest portion of the plant, it suffers most from accidental injuries, the attacks of aquatic animals (e. g., insects, snails, planarians) and from other injurious factors. Consequently, when one deals with comparatively few individual plants the results are bound to be irregular, because the proportion of unmutilated whorls in different regions of the main stem will differ from plant to plant. In spite of this irregularity in the constants for different individual plants, however, we are able to reach certain definite results.

In the first place, it is quite clear, whether we compare single plants or series, that the mean number of leaves to the whorl is higher for the

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whorls on the main stem than for the plant as a whole. Further, we see that both absolutely and relatively the main-stem whorls are on the whole distinctly less variable than are those from the entire plant taken together. But obviously the fair comparison is not between main-stem whorls and all whorls in the plant, but between main-stem whorls and all whorls on branches. Accordingly we may examine the distributions and their constants for the whorls on all branches of the plant. In table 7 are given the frequency distributions for variation in such whorls for the totals for the six series. It is not necessary to tabulate these distributions for each plant separately, for reasons which will appear as we go on.

TABLE 7.—*Frequency distributions for variation in leaf-number in whorls on all branches. Totals for series.*

Series.	Plant.	Distribution number.	Leaves per whorl.										
			3	4	5	6	7	8	9	10	11	12	Total.
I	All plants	43	...	...	3	56	92	184	219	134	9	...	697
II	do	60	...	...	3	64	108	187	258	194	9	...	823
III	do	72	...	...	...	44	49	98	148	94	1	...	434
IV	do	96	1	...	1	19	171	329	531	392	6	...	1,450
V	do	138	...	4	28	42	120	113	145	82	2	...	536
VI	do	175	...	...	9	23	67	111	127	190	9	1	537
I, II, III, combined	do	181	...	...	6	164	249	469	625	422	19	...	1,954

The difference between these distributions and the corresponding ones for the main stem given in table 5 is apparent. The "all-branch" distributions resemble closely those for the plant as a whole. The most frequently occurring whorls are those with 9 leaves (except in Series VI) as against 10 in the case of the main-stem whorls. The constants for the "all-branch" distributions are given in table 8.

TABLE 8.—*Constants for variation in leaf-number in whorls on all branches. Totals for series.*

Series.	Plant.	Distribution number.	Mean (unit—1 leaf).	Standard deviation (unit—1 leaf).	Coefficient of variation.
I	All plants	43	8.432±0.031	1.227±0.022	14.550±0.268
II	do	60	8.520± .029	1.249± .021	14.657± .249
III	do	72	8.465± .040	1.237± .028	14.611± .342
IV	do	96	8.770± .018	1.042± .013	11.885± .151
V	do	138	8.021± .042	1.429± .024	17.819± .447
VI	do	175	8.741± .038	1.315± .027	15.047± .317

It is at once apparent that the whorls on the main stem have on the average a higher number of leaves than do whorls on branches. Further,

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main-stem whorls are distinctly less variable, both absolutely and relatively. That these changes are significant is shown in table 9, which may be called a "difference table." It gives for any designated series the difference (and its probable error) between the value of a particular constant for the whorls on all branches of that series as given in table 8, and the value of the same constant for the main-stem whorls of the same series. The absolute differences, expressed as per cent of the constant for the "all-branch" series, are tabulated as "relative differences." The sign of a difference is taken positive when the main-stem constant is the greater.

TABLE 9.—*Difference table, comparing main-stem whorls with whorls on all branches. Totals for series.*

Series.	Differences.	Between means (unit—1 leaf).	Between standard deviations (unit—1 leaf).	Between coefficients of variation.
I	Absolute difference	0.885±0.061	—0.165±0.044	—3.153±0.490
	Relative difference..per cent..	10.5	— 13.4	— 21.7
II	Absolute difference	1.232± .060	— .447± .043	—6.432± .459
	Relative difference..per cent..	14.5	— 35.6	— 43.9
III	Absolute difference	1.254± .063	— .550± .045	—7.545± .496
	Relative difference..per cent..	14.8	— 44.5	— 51.7
IV	Absolute difference	.742± .076	— .339± .039	—4.498± .419
	Relative difference..per cent..	8.5	— 32.5	— 37.8
V	Absolute difference	.713± .089	— .146± .060	—3.125± .783
	Relative difference..per cent..	8.9	— 10.2	— 17.5
VI	Absolute difference	.348± .075	— .103± .053	—1.709± .606
	Relative difference..per cent..	4.0	— 7.6	— 11.4

There can be no doubt that these differences are significant in comparison with their probable errors. The only cases in which the differences are not more than three times the probable errors are for the standard deviations of Series V, and the standard deviations and the coefficients of variation of Series VI. Even in these cases the differences are more than twice the probable errors. *There is a very substantial differentiation between main-stem whorls and whorls borne on branches.* Main-stem whorls have on the average roughly 1 leaf more than do whorls on branches, and are from 10 to 50 per cent less variable, both absolutely and relatively. The very low variability of main-stem whorls both absolutely and as compared with whorls on other portions of the plant may be brought out by a totally different sort of consideration. We say with regard to any organ or character that it varies very little if the chance of finding any other than the typical condition is small. If the chance of the occurrence of deviations from the typical condition is large, we say that there is great variation. Now, in the case

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of whorls on the main stems of Ceratophyllum plants, the chance that a whorl chosen at random will have 10 leaves is, on the basis of the combined Series I, II, and III, $\frac{5}{1}\frac{2}{0}\frac{1}{0}\frac{}{0}$. Or, in other words, the chance in favor of the 10-leaved whorl is *greater than the combined chance of all other whorls together*. This means, of course, very low variability.

In order to gain a more precise idea of the nature of this differentiation I propose to treat the distributions analytically. In doing this I shall, as before, combine the frequency distributions for Series I, II, and III. These series are so slightly differentiated from one another that the error made by combining them is altogether negligible. In fact it is practically certain that we shall come nearer to the true facts by using the combined data for these three series from the same locality than by taking any one of them separately. For the same reasons as before I have used the raw moments in determining the constants. The analytical results for "main-stem" and "all-branch" whorls are given in table 10. The combined distributions are, for the main-stem whorls, No. 180 in table 5, and for the whorls on branches, No. 181 of table 7.

TABLE 10.—*Analytical constants for variation in leaf-number. Series I, II, and III combined.*

Constant.	Main-stem whorls (Distribution No. 180).	Whorls on all branches (Distribution No. 181).	Constant.	Main-stem whorls (Distribution No. 180).	Whorls on all branches (Distribution No. 181).
Total frequency..	374	1,954	Skewness	—0.4270	—0.6119
μ_2.....	.8798	1.5350	Modal divergence	— .4005	— .7581
μ_3.....	— .9013	— .8739	Standard deviation	.9380	1.2390
μ_4.....	4.0691	5.8052	Mean	9.5348	8.4765
β_1.....	1.1928	.2112	Mode	9.9353	9.2345
$\sqrt{\beta_1}$.....	1.0921	.4595	Range.....	.....	6.0426
β_2.....	5.2568	2.4637	Lower end of range	.....	4.5435
β_2—3	2.2568	— .5363	Upper end of range	13.2096	10.5861
κ_1.....	+ .9354	—1.7060			
κ_2.....	+1.2455	.....			

This table brings out clearly the essential differences between "main-stem" and "all-branch" whorls in respect to variation in leaf-number. We note at once that the main-stem distribution is markedly less skew than is the branch distribution, the distance from mean to mode being in the former case only a little more than half what it is in the latter. The direction of the skewness is the same however, in both cases, namely negative, or the mode is larger than the mean. The range for the "all-branch" distribution is, as was to be expected, less than what it is for the plant as a whole (cf. table 4).

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For the "all-branch" distribution the criterion κ_1 $(=2\beta_2-3\beta_1-6)$ is negative, indicating that a curve of Type I is demanded for graduation. In the case of the main-stem distribution, however, κ_1 is positive, whence at first thought it would be concluded that a curve of Type IV was demanded. But it has been shown by Pearson (:01) that κ_1 positive, while a necessary condition, is not a sufficient condition for Type IV.

In addition,

$$\kappa_2=\frac{\beta_1(\beta_2+3)^2}{4(4\beta_2-3\beta_1)(2\beta_2-3\beta_1-6)}$$

must be >0 and <1. We see at once that the main-stem distribution does not fulfill this latter condition, since $\kappa_2=1.2455$, or is >1. Clearly, then, one of the transition curves of Type V or Type VI is wanted. The condition for Type V is that $\kappa_2=1$, while for Type VI we must have $\kappa_2>1$ and $<\infty$. Strictly speaking, then, our main-stem distribution should be graduated by a curve of Type VI, but insomuch as κ_2 differs from 1 by only a small amount we shall probably get sufficiently good results with Type V. I have accordingly fitted the main-stem distribution with a Type V curve and the "all-branch" distribution with a Type I curve. The equations to the curves are:

Main-stem distribution (Type V):[1]

$$\text{Log } y=19.6849467-18.34909 \text{ log } x-26.092355\left(\frac{1}{x}\right)$$

Origin at 13.2096; x positive towards small whorls.

All branch distribution (Type I):

$$y=581.6454\left(1+\frac{x}{4.6910}\right)^{1.8672}\left(1-\frac{x}{1.3515}\right)^{.5880}$$

Origin at mode = 9.2345.

The histograms and their fitted curves are shown in fig. 7. The frequencies for both curves were reduced to percentages before plotting, so that, since the base elements are the same, both curves have the same area in the diagram. This method brings out most clearly the points of difference between the two distributions.

[1]For obvious reasons I have put the curve in the logarithmic form. The equation to a curve of this type is of the form

$$y=y_0x^{-p}e^{-\gamma/x}$$

where y_0, p, and γ are constants.

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It is evident that the graduations are as good as could reasonably be expected, considering the small number of classes from which the moments had to be calculated.

I wish now to consider more fully a point that was raised earlier in the paper. In the section dealing with the methods used in collecting the material it was pointed out (p. 11) that in some cases the main stem of a plant divided, forming what we have called secondary main stems, and in some cases even a secondary main-stem was divided to form

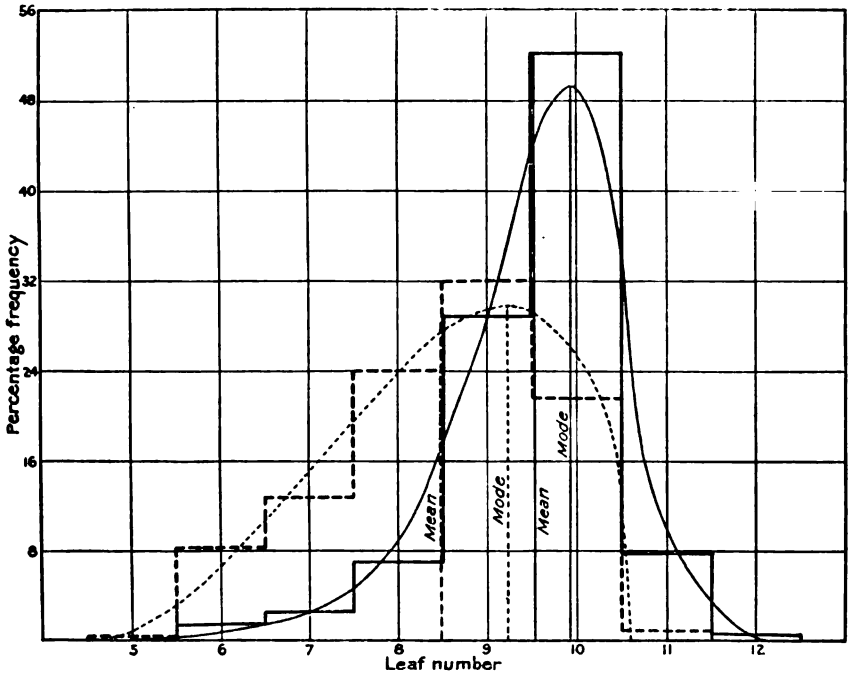

FIG. 7.—Frequency histograms and fitted curves for variation in leaf-number in main-stem and "all-branch" whorls of Series I, II, and III combined. Main-stem distribution and curve in solid lines; "all-branch" distribution and curve in broken lines.

"tertiary" stems. The statement was made that there was no difficulty in practice in distinguishing such main stem divisions from primary lateral branches. I wish now to present statistical evidence to indicate that the variation in leaf-number in these portions of the plants shows that they are parts of the main stem rather than branches.

In table 11 are given the frequency distributions for all the secondary main-stem whorls which were found in the course of the work, and in table 12 are given the distributions for tertiary main-stem whorls.

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It is evident from these tables that division of the main stem occurred relatively infrequently in our material. All plants of Series II, V, and VI and and three out of five plants of Series I had the main stem undivided. Plant 1, Series III and both plants of Series IV had long secondary main stems. In these plants the main stem proper was very short, bearing only a few whorls. In the case of plant 2, Series IV, there were no unmutilated whorls on the main stem below the point of

TABLE 11.—*Frequency distributions for variation in leaf-number of whorls on secondary main stems.*

Series.	Plant.	Distribution number.	Leaves per whorl.					
			7	8	9	10	11	Total.
I	1	182	...	1	3	10	...	14
	3	183	1	2	8	13	1	25
	All plants.	16	1	3	11	23	1	39
III...	1	66	...	1	11	51	6	69
IV	1	184	...	4	6	18	...	28
	2	185	...	1	2	2	...	5
	All plants.	80	...	5	8	20	...	33

TABLE 12.—*Frequency distributions for variation in leaf-number of whorls on tertiary main stems.*

Series.	Plant.	Distribution number.	Leaves per whorl.					
			6	7	8	9	10	Total.
I	1	186	...	1	2	9	13	25
	3	187	1	2	3	4	2	12
	All plants.	23	1	3	5	13	15	37
IV...	2	81	...	1	2	15	27	45

division. The distributions exhibit even on casual inspection a marked difference from what has been shown to be characteristic for the variation of whorls on branches. These differences are brought out in a still more striking way by the constants of the distributions, which are given in table 13.

Now, I think it is perfectly obvious if we compare the values given in this table with those for the "all-branch" distributions given in table 8, or with those for the primary, secondary, or tertiary branches given in tables 15, 18, and 23, *infra*, that the whorls on those divisions of the

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plant which we have called "secondary" and "tertiary" main stems are sensibly differentiated from whorls borne on any branches, of whatever order. These whorls have a higher mean number of leaves and are markedly less variable (absolutely and relatively) than are whorls on branches. That is, they have those characters which we have just seen hold for main-stem whorls generally. There can be, I believe, but one conclusion, namely, that these portions of the plant are parts of the main stem rather than primary branches.

The results of this section of the paper may be summarized as follows:

It has been shown that (1) whorls borne on the main stem of the plant have a significantly higher mean and modal number of leaves than do whorls borne on branches; (2) main-stem whorls are markedly less variable, both absolutely and relatively, than are whorls borne on branches; (3) the distribution of variation in leaf-number is distinctly less skew

TABLE 13.—*Constants for variation in leaf-number in whorls on secondary and tertiary main stems.*

Series.	Plant and portion.	Distribution number.	Mean (unit — 1 leaf).	Standard deviation (unit—1 leaf.)	Coefficient of variation.
I	1 and 3, secondary main stem..	16	9.513±0.084	0.780±0.060	8.202±0.631
	1 and 3, tertiary main stem	23	9.027± .117	1.052± .083	11.657± .926
III...	1, secondary main stem	66	9.899± .044	.542± .031	5.478± .315
IV	1 and 2, secondary main stem..	80	9.455± .087	.742± .062	7.851± .655
	2, tertiary main stem.....	81	9.511± .069	.687± .049	7.224± .515

in the case of the main-stem whorls than in whorls borne on branches; (4) the divisions of the main stem have the same characteristics in respect to variation in leaf-number that the main stem proper does.

From these facts we conclude that *whorls borne on the main stem of the plant are, as a class, clearly differentiated from whorls borne on branches.*

VARIATION IN WHORLS ON PRIMARY BRANCHES.

Anyone familiar with Ceratophyllum will recognize that it is the primary branches which make up the greater portion of the plant. They usually contribute a considerably larger number of whorls to the total than does any other single division. This fact will be apparent by comparing the data of table 14, which gives the frequency distributions for primary branches, with those in the tables for other divisions of the plant.

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Comparing these distributions with those given in table 1, it is at once evident that there is a great similarity. The most frequently occurring whorls in both cases are those with 9 leaves. The range of variation is practically the same for the primary branches as it is for

TABLE 14.—*Frequency distributions for variation in leaf-number of whorls on primary branches.*

Series.	Plant.	Distribution number.	Leaf-number per whorl.										
			3	4	5	6	7	8	9	10	11	12	Total.
I	1	25	...	...	1	9	18	29	43	34	1	...	135
	2	26	...	...	1	4	10	25	27	27	4	...	98
	3	27	...	...	1	11	9	26	37	12	2	...	98
	4	28	...	...	...	7	22	47	53	42	1	...	172
	5	29	...	...	...	1	3	14	17	10	1	...	46
	All plants	30	...	...	3	32	62	141	177	125	9	...	549
II	1	50	...	...	...	19	46	79	114	102	2	...	362
	2	51	...	...	1	10	25	47	64	63	6	...	216
	All plants	52	...	...	1	29	71	126	178	165	8	...	578
III	1	68	...	...	...	13	25	59	76	59	1	...	233
IV	1	83	...	...	...	3	19	62	136	127	2	...	349
	2	84	1	...	1	7	46	82	187	139	2	...	465
	All plants	85	1	...	1	10	65	144	323	266	4	...	814
V	1	113	...	2	9	17	33	10	54	32	2	...	159
	2	114	...	...	...	...	1	...	...	...	...	...	1
	3	115	...	...	...	...	1	6	3	2	...	...	12
	4	116	...	...	...	...	2	3	4	...	...	...	9
	5	117	...	...	...	...	5	6	1	...	...	...	12
	6	118	...	...	...	2	4	8	23	10	...	...	47
	7	119	...	...	...	7	24	15	22	7	...	...	75
	All plants	120	....	2	9	26	70	48	107	51	2	...	315
VI	1	153	...	...	...	2	...	7	10	9	...	...	28
	2	154	...	...	2	3	8	11	8	3	...	...	35
	3	155	...	...	...	5	5	7	10	2	1	...	30
	4	156	...	...	...	1	7	8	5	2	...	...	23
	5	157	...	...	2	2	18	24	23	31	...	...	100
	6	158	...	...	2	2	9	16	24	85	6	1	145
	All plants	159	...	...	6	15	47	73	80	132	7	1	361
I, II, III	All plants	188	...	...	4	74	158	326	431	349	18	...	1,360

the whole plant. In fact, these distributions make it clear that the characteristic features of the variation of the plant as a whole with respect to leaf-number are very largely determined by the primary branches. The same essential similarity as before is observed when

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we compare the first four series. This is so evident from the distributions themselves and from the values of the constants which follow that it does not appear to be necessary to figure separately the polygons of variation in the primary branches. The general character of the distributions is shown graphically in fig. 8, p. 44, in which primary and secondary branches are compared in respect to variation in leaf-number.

From distribution 84 it is seen that the single 3-leaved whorl observed in the course of the work was situated on a primary branch. In Series VI, the single 12-leaved whorl of that series was on a primary branch. Thus it would appear that the whole range of variation in leaf-number in Ceratophyllum may be shown by primary-branch whorls.

TABLE 15.—*Constants for variation in leaf-number in whorls on primary branches.*

Series.	Plant.	Distribution number.	Mean (unit—1 leaf).	Standard deviation (unit — 1 leaf).	Coefficient of variation.
I	1	25	8.556±0.072	1.245±0.051	14.555±0.610
	2	26	8.735± .085	1.250± .060	14.310± .703
	3	27	8.337± .085	1.253± .060	15.031± .740
	4	28	8.605± .058	1.124± .041	13.057± .483
	5	29	8.761± .100	1.004± .071	11.460± .816
	All plants	30	8.581± .035	1.199± .024	13.976± .290
II	1	50	8.663± .042	1.179± .030	13.605± .347
	2	51	8.741± .056	1.228± .040	14.044± .465
	All plants	52	8.692± .034	1.198± .024	13.780± .278
III	1	68	8.627± .051	1.147± .036	13.296± .423
IV	1	83	9.063± .033	.925± .024	10.206± .263
	2	84	8.867± .033	1.057± .023	11.923± .267
	All plants	85	8.951± .024	1.007± .017	11.254± .190
V	1	113	8.138± .086	1.608± .061	19.754± .776
	7	119	7.973± .091	1.166± .064	14.622± .822
	All plants	120	8.184± .053	1.386± .037	16.938± .468
VI	2	154	7.829± .145	1.276± .103	16.297±1.348
	5	157	8.570± .085	1.259± .060	14.691± .715
	6	158	9.359± .066	1.178± .047	12.592± .506
	All plants	159	8.759± .047	1.332± .033	15.202± .390

The chief physical constants for the distributions of table 14 are given in table 15.

As we should expect, the values of the constants for primary branches throughout are of the same order as those for the "all-branch" distri-

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butions given in table 8. We note, however, that primary-branch whorls by themselves are somewhat less variable, both absolutely and relatively, than are the "all-branch" whorls. The means are also slightly higher in the primary-branch than in the "all-branch" distributions. This definite system of differences would appear to indicate that whorls on primary branches are as a class differentiated from whorls on other branch divisions of the plant. It will be seen later that this is the case. It should be noted how slight the differences are between the constants for Series I, II, and III, for the portion of the plant under consideration. The means for the three series differ by 0.1 leaf or less, and the standard deviations by < 0.06 leaf. It is clear that these differences are only what would be expected to arise from random sampling, and that there is no sensible, *real* differentiation between these series. As has been the case in the other portions of the plant so far examined, there is a definite, though not large, divergence between the constants for Series IV and those for Series I, II, and III. Series V and VI fall in a class by themselves.

TABLE 16.—*Difference table comparing primary-branch whorls with main-stem whorls. Totals for series.*

Series.	Differences.	Between means (unit = 1 leaf)	Between standard deviations (unit = 1 leaf).	Between coefficients of variation.
I	Absolute difference	−0.736±0.064	0.137±0.045	2.579±0.502
	Relative difference..per cent...	7.9	12.9	22.6
II	Absolute difference	−1.060± .063	.396± .044	5.555± .475
	Relative difference..per cent...	10.9	49.4	67.5
III	Absolute difference	−1.092± .071	.460± .050	6.230± .555
	Relative difference..per cent...	11.2	67.0	88.2
IV	Absolute difference	− .561± .078	.304± .041	3.867± .435
	Relative difference..per cent...	5.9	43.2	52.3
V	Absolute difference	− .550± .093	.103± .066	2.244± .795
	Relative difference..per cent...	6.3	8.0	15.3
VI	Absolute difference	− .330± .080	.120± .057	1.864± .648
	Relative difference..per cent...	3.6	9.9	14.0

The main-stem whorls form a definite base with which the primary-branch whorls may be compared. This comparison is made in table 16, which is a "difference table" corresponding in plan to table 9 above. In this case the differences are given the positive sign when the primary-branch constant is the greater. The relative difference is in each case the percentage which the absolute difference is of the main-stem constant. Only the totals for the series are compared.

Considering the first four series, we see that both absolute and relative differences are large. There can be no doubt that they are significant. In Series V and VI the differences are smaller, but still probably in all cases significant. We conclude, then, that primary-branch whorls as

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compared with main-stem whorls have on the average nearly one less leaf to the whorl, and are relatively 20 to 80 per cent more variable.

The analytical consideration of the variation in primary-branch whorls will be taken up later in connection with the secondary-branch distributions.

It is shown in this section that *whorls on primary branches are as a class differentiated from whorls borne on the main stem. As we pass from main-stem whorls to primary-branch whorls the mean number of leaves in the whorl decreases and the variability increases.*

VARIATION IN WHORLS ON SECONDARY BRANCHES.

The frequency distributions for the variation in leaf-number in this portion of the plant are given in table 17.

TABLE 17.—*Frequency distributions for variation in leaf-number in whorls on secondary branches.*

Series.	Plant.	Distribution number.	Leaves per whorl.								
			4	5	6	7	8	9	10	11	Total.
I	1	31	...	...	2	6	11	3	1	...	23
	2	32	...	...	5	5	4	24	8	...	46
	3	33	...	...	5	4	4	3	...	...	16
	4	34	...	...	10	12	24	12	...	...	58
	All plants.	35	...	...	22	27	43	42	9	...	143
II	1	53	...	2	26	21	40	63	24	1	177
	2	54	...	...	6	12	16	16	4	...	54
	All plants.	55	...	2	32	33	56	79	28	1	231
III	1	69	...	...	24	19	34	60	28	...	165
IV	1	86	...	...	...	34	73	86	33	1	227
	2	87	...	...	9	64	105	119	92	1	390
	All plants.	88	...	...	9	98	178	205	125	2	617
V	1	121	2	7	4	22	14	15	12	...	76
	7	122	...	1	3	5	8	7	4	...	28
	All plants.	123	2	8	7	27	22	22	16	...	104
VI	1	160	...	...	3	6	6	12	12	...	39
	2	161	...	...	1	2	4	...	...	...	7
	5	162	...	2	3	4	9	13	21	...	52
	6	163	...	...	...	4	11	9	24	2	50
	All plants.	164	...	2	7	16	30	34	57	2	148
I, II, III	All plants.	189	...	2	78	79	133	181	65	1	539

It is apparent from the totals of this table that secondary branches (in the present material at least) contribute less than half as many

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whorls to the total number borne by Ceratophyllum plants than do primary branches. Also, one notes that the character of the distributions is changing. While the most frequently occurring whorls on the secondary branches are, as in the case of the primaries, those having 9 leaves, yet whorls with fewer than 9 leaves occur proportionately much more frequently on secondary than on primary branches. We should expect, then, that the average number of leaves to the whorl would be less for the secondaries than for the primaries. That this is in fact the case is shown in table 18. Series V and VI still maintain their peculiar character. In Series V the actually most frequent whorls are those having 7 leaves, though 8 and 9 leaved whorls are nearly as frequent. Series VI has the greatest frequency at 10, as in the case of the primaries.

TABLE 18.—*Constants for variation in leaf-number in whorls on secondary branches.*

Series.	Plant.	Distribution number.	Mean (unit = 1 leaf).	Standard deviation (unit = 1 leaf).	Coefficient of variation.
I	1	31	7.783±0.131	0.930±0.093	11.956±1.206
	2	32	8.543± .120	1.211± .085	14.170±1.016
	4	34	7.655± .088	.992± .062	12.962± .825
	All plants	35	7.923± .065	1.159± .046	14.631± .596
II	1	53	8.198± .066	1.311± .047	15.989± .587
	2	54	8.000± .103	1.122± .073	14.027± .928
	All plants	55	8.152± .056	1.272± .040	15.603± .501
III	1	69	8.297± .067	1.285± .048	15.487± .589
IV	1	86	8.533± .042	.930± .029	10.904± .349
	2	87	8.574± .037	1.095± .026	12.767± .313
	All plants	88	8.559± .028	1.037± .020	12.121± .236
V	1	121	7.737± .123	1.584± .087	20.476±1.166
	All plants	123	7.817± .101	1.524± .071	19.494± .946
VI	5	162	8.750± .131	1.399± .093	15.987±1.084
	6	163	9.180± .102	1.071± .072	11.669± .798
	All plants	164	8.797± .072	1.294± .051	14.712± .589

We see in this case as before a close similarity between the results for Series I, II, and III. Series V shows the highest variabilities for this portion of the plant, and Series VI the highest means. Comparing the results with those for primary branches, it appears that secondary-branch whorls have fewer leaves to the whorl and are more variable than those on primaries. The nature and the extent of the differences

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are shown in table 19. In this "difference table" the differences are taken as positive when the primary-branch constant is the greater and negative when the constant for the secondaries is the greater. The absolute differences are taken as percentages of the primary-branch constant, in each case, to obtain the relative differences.

TABLE 19.—*Difference table comparing secondary with primary-branch whorls. Totals for series.*

Series.	Differences.	Between means (unit — 1 leaf).	Between standard deviations (unit — 1 leaf).	Between coefficients of variation.
I	Absolute difference	0.658±0.074	0.040±0.052	—0.655±0.663
	Relative difference..per cent..	7.67	3.33	4.7
II	Absolute difference	.540± .066	— .074± .047	—1.823± .573
	Relative difference..per cent..	6.21	6.17	13.2
III	Absolute difference	.330± .084	— .138± .060	—2.191± .725
	Relative difference..per cent..	3.83	12.03	16.5
IV	Absolute difference	.392± .037	— .030± .026	— .867± .303
	Relative difference..per cent..	4.36	2.97	7.7
V	Absolute difference	.367± .114	— .138± .080	—2.556±1.055
	Relative difference..per cent..	4.48	9.95	15.1
VI	Absolute difference	— .038± .086	.038± .061	.490± .706
	Relative difference..per cent..	.43	2.85	3.2

We see that generally the differences are positive in the "mean" column and negative in the two variability columns, thus indicating what was pointed out above, that whorls on secondary branches have fewer leaves to the whorl and tend to be more variable than those on primary branches. In respect to variation in leaf-number, then, the secondary branches stand in much the same relation to the primaries as the latter do to the main stem. In one case, Series VI, the order of the differences is reversed, the mean being higher and the variability lower for the secondary-branch whorls than for the primary, but no special stress can be laid on this apparent exception to the rule, because the differences are altogether insignificant in comparison with their probable errors. The differences between the means are, with this single exception, significant in comparison with their probable errors. In the variability columns the individual differences when taken singly are in most cases not certainly significant. Due weight must, however, be given to the fact that all tend in the same direction (except of course Series VI). I think we may safely conclude that, in general, whorls on secondary branches are as a class more variable in respect to leaf-number than are whorls on primary branches.

We may now consider analytically the variation in primary and secondary branch whorls, in comparison with each other and with whorls on the main stem. As in other cases I have used the combined distri-

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butions for Series I, II, and III in the analytical treatment. The justification for combining these three sets of data will have been apparent to anyone who has inspected the values of the constants which have been given in the preceding tables. The "raw" moments were used in this as in the other cases. The values of the chief physical and algebraical constants of distributions 188 and 189 of tables 14 and 17 are given in table 20.

TABLE 20.—*Analytical constants for variation in leaf-number. Series I, II, and III combined.*

Constant.	Primary-branch whorls (Distribution No. 188).	Secondary-branch whorls (Distribution No. 189).	Constant.	Primary-branch whorls (Distribution No. 188).	Secondary-branch whorls (Distribution No. 189).
Total frequency	1360	539	Skewness	—0.5484	—0.9996
μ_2	1.4183	1.5753	Modal divergence	— .6530	—1.2547
μ_3	— .8671	— .6964	Standard deviation	1.1909	1.2551
μ_4	5.3199	5.3816	Mean	8.6360	8.1354
β_1	.2636	.1240	Mode	9.2891	9.3901
$\sqrt{\beta_1}$	.5134	.3522	Range	6.5021	5.1929
β_2	2.6448	2.1685	Lower end of range	4.2354	5.1923
$\beta_2 - 3$	— .3552	— .8315	Upper end of range	10.7375	10.3852
κ_1	—1.5011	—2.0351			

From this table we note that:

(*a*) The distribution for the secondary branches is markedly more skew than is that for the primaries. Consequently, since the standard deviation is also greater in the case of the secondary branches, we find that—

(*b*) The distance from the mean to the mode is very nearly twice as great in the secondary branches as it is in the primaries.

(*c*) Secondary branches have a lower mean number of leaves to the whorl, but a higher modal number than the primaries. Too much stress must not, however, be laid on the fact that the secondaries show the higher modal number, because, as has been pointed out, the values of the moments from which the mode has to be calculated have not been in any way corrected.

(*d*) The theoretical range of variation is smaller for secondary branches than it is for primaries by more than one leaf. The secondary curve starts at a higher and ends at a lower value than does the primary.

(*e*) The skewness is negative for both curves.

(*f*) The kurtosis ($\eta = \beta_2 - 3$) is negative in both curves, but has a considerably higher value in the case of the secondary branches, thus indicating that the secondary-branch distribution is the more flat-topped.

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(*g*) Both curves are of Type I, the equations being as follows:

Distribution No. 188, primaries:

$$y = 433.4048\left(1 + \frac{x}{5.0536}\right)^{2.7363}\left(1 - \frac{x}{1.4484}\right)^{.78}$$

Distribution No. 189, secondaries:

$$y = 151.1892\left(1 + \frac{x}{4.1978}\right)^{.8726}\left(1 - \frac{x}{.9951}\right)^{.2063}$$

The curves are shown graphically in fig. 8. The frequencies are reduced to percentages, so that both curves have the same area in the diagram. The greater skewness of the secondary distribution is very evident from the diagram.

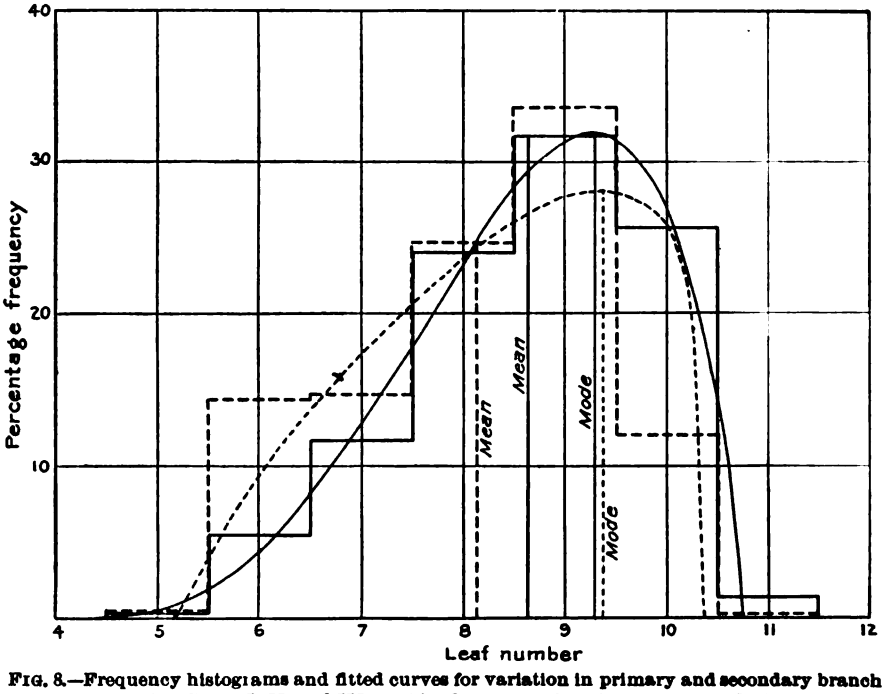

FIG. 8.—Frequency histograms and fitted curves for variation in primary and secondary branch whorls. Series I, II, and III combined. —— primaries; - - - - secondaries.

It is interesting to note that the analytical results give a greater range of variation for primary than for secondary branches. This is what we should expect on general principles to find, because the primary branches are so much longer, and consequently bear so many more whorls, than do the secondaries.

Comparing the results for primary branches with those for the main stem given in table 10 (p. 32) we note that (*a*) the variation is dis-

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tinctly more skew in the whorls on primary branches than in those in the main stem; (*b*) the primary-branch whorls are the more variable; (*c*) the *mean* number of leaves per whorl is 0.8988 higher in the main-stem than in the primary-branch whorls, while the *modal* number of leaves per whorl is only 0.6462 higher; (*d*) the sign of the kurtosis changes in passing from main-stem to primary branches.

From the results presented in this section we may conclude that *whorls borne on secondary branches are as a class differentiated from those borne on either the main stem or primary branches.* The changes in the constants as we pass from primary to secondary branches are similar in kind to those which we find in passing from main-stem to primary-branch whorls. The most important of these changes are (1) the lowering of the mean number of leaves to the whorl, and (2) the increase in the variation in this character.

VARIATION IN WHORLS ON TERTIARY AND QUATERNARY BRANCHES.

As the number of whorls is comparatively small in these portions of the plant we may conveniently consider tertiary and quaternary branches together. It will be understood that by "tertiary branches" are meant those which arise from secondary branches, and by "quaternary" those which arise from tertiaries.

TABLE 21.—*Frequency distributions for variation in leaf-number in whorls on tertiary branches.*

Series.	Plant.	Distribution number.	Leaves per whorl.						
			5	6	7	8	9	10	Total.
I...	2 and 4.....	36	...	2	3	...	...	...	5
II...	1.....	56	...	3	4	5	1	1	14
III...	1.....	70	...	7	5	5	12	7	36
IV	1.....	89	...	...	1	1	...	...	2
	2.....	90	...	...	7	6	3	1	17
	All plants..	91	...	...	8	7	3	1	19
V	1..... ...	124	7	5	12	18	11	11	64
	7.....	125	...	1	1	4	1	...	7
	All plants..	126	7	6	13	22	12	1	71
VI	1.....	165	...	...	1	1	2	1	5
	5.....	166	1	1	3	7	11	...	23
	All plants.	167	1	1	4	8	13	1	28

The frequency distributions for tertiary and quaternary branches are given in tables 21 and 22, respectively.

The totals here are so small that much regularity in the distributions can not be expected, nor can very accurate comparisons between

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the constants be made, because of the large probable errors. It is of interest to note that the number of tertiary whorls is greater in Series III, than in Series II or I. The relative increase is greater than is indicated by the figures in table 21, since the total of Series III is smaller than that of either I or II. This increase in tertiary whorls is a rough index of the change which took place in the Carp Lake population, due to growth in the interval between the collection of Series I and Series III.

TABLE 22.—*Frequency distributions for variation in leaf-number in whorls on quaternary branches.*

Series.	Plant.	Distribution number.	Leaves per whorl.						
			5	6	7	8	9	10	Total
V	1.....	127	4	2	9	18	2	4	39
	7.....	128	...	1	1	3	2	...	7
	All plants..	129	4	3	10	21	4	4	46

In order that some judgment may be formed of the characteristics of tertiary-branch whorls I have prepared table 23, which gives, in addition to the constants for the distributions of table 21, the absolute differences between these and the constants for secondary-branch whorls. Only totals for series are tabled, because of the paucity of material. The difference is taken as positive when the secondary-branch constant is the greater.

The probable errors are very large, as was to be expected, and the results are not as smooth as could be desired. Still, I think, we may safely draw the following conclusions:

(*a*) The mean number of leaves to the whorl is distinctly lower for tertiary than for secondary branch whorls. In only one case out of the five is the difference between the means negative, and then it is sensibly zero, in comparison with its probable error. In Series II, IV, and VI, the difference is 0.6 to 0.7 leaf, a very considerable amount, and certainly significant in comparison with the probable error. It is of the same order as the difference between main-stem and primary-branch whorls (cf. table 16), and is distinctly greater than the difference between primary and secondary branches in respect to mean number of leaves per whorl.

(*b*) The tertiary-branch whorls tend on the whole to be less rather than more variable than those borne on secondaries. The differences in the variability columns are all very small, and, taken singly, quite insignificant in comparison with their probable errors. Due weight, however, must be given to the fact that the sign of the differences is uniformly

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plus. In fact, Series III forms the only exception to this rule. This exception arises from the fact shown in table 28, p. 52 that the tertiary branches tend to be more variable in length than is the case in the other series. It will be shown in later sections of the paper that the positional differentiation of whorls within an axial division of the plant is such that the variation exhibited by groups of whorls may be greatly influenced by the length of the branches on which they are borne.

TABLE 23.—*Constants for variation in whorls on tertiary branches. Totals for series.*

Series.	Portion of plant.	Distribution number.	Mean.	Standard deviation.	Coefficient of variation.
II	Secondary branches	55	8.152±0.056	1.272±0.040	15.608±0.501
	Tertiary branches..	56	7.500± .202	1.118± .142	14.907±1.942
	Difference.....	.....	+ .652± .210	+ .154± .148	+ .696±2.006
III	Secondary branches	69	8.297± .067	1.285± .048	15.487± .589
	Tertiary branches..	70	8.194± .159	1.411± .112	17.215±1.408
	Difference.....	.....	+ .103± .173	— .126± .122	—1.728±1.526
IV	Secondary branches	88	8.559± .028	1.037± .020	12.121± .236
	Tertiary branches..	91	7.842± .135	.874± .096	11.150±1.235
	Difference.....	.....	+ .717± .138	+ .163± .098	+ .971±1.257
V	Secondary branches	123	7.817± .101	1.524± .071	19.494± .946
	Tertiary branches..	126	7.831± .119	1.473± .083	18.805±1.101
	Difference.....	.....	— .014± .156	+ .051± .109	+ .689±1.452
VI	Secondary branches	164	8.797± .072	1.294± .051	14.712± .589
	Tertiary branches..	167	8.021± .140	1.102± .099	13.785±1.261
	Difference.....	.....	+ .776± .157	+ .192± .111	+ .977±1.392

(*c*) The tertiary-branch whorls thus appear to be differentiated as a class from those borne on other portions of the plant.

Turning to the whorls on quaternary branches, we have, unfortunately, only a single series which gives any data at all. In our experience the extreme condition of lateral growth implied in quaternary and higher order branches is very rare. It seems possible that this may be due merely to the restriction imposed by the shortness of the growing season. The finding of quaternary branches in the plants of Series V lends support to this view, for the reason that, as has been pointed out above (p. 15) the large plants in this series had wintered over and were growing like perennials. An examination of Ceratophyllum from more southern latitudes would be interesting in this connection.

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The constants for the quaternary-branch whorls of Series V are given in table 24, together with their differences when compared with tertiary-branch whorls.

TABLE 24.—*Constants for variation in whorls on quaternary branches. Series V.*

Distribution number.	Portion of plant.	Mean.	Standard deviation.	Coefficient of variation.
126	Tertiary branches.....	7.831±0.119	1.473±0.083	18.805±1.101
129	Quaternary branches.....	7.652± .125	1.255± .088	16.989±1.225
	Difference	+ .179± .173	+ .218± .121	+1.866±1.647

We see that the mean number of leaves in the quaternary-branch whorls is less than in those on tertiaries. The difference, however, is small, being of the same order as its probable error. The quaternary-branch whorls are also slightly the less variable. In the case of the standard deviations the difference is nearly twice its probable error. We may conclude, provisionally at least, that the same kind of change occurs in the mean when we pass from tertiary to quaternary branches as when we pass from secondaries to tertiaries. The differences between the constants for whorls on these higher-order branches in any case would probably be small in absolute amount, for reasons which will appear as we go on.

THE RELATIVE SIZE OF THE DIFFERENT DIVISIONS OF THE PLANT AND THE VARIATION IN THIS CHARACTER.

It will readily be admitted that if we are to get any light on the question of the factors which produce the characteristic frequency distributions of variation for the whorls of a particular division of the plant, by a study of the laws of growth and differentiation of the whorls themselves, it will be necessary to know in addition something about what proportions of the total whorls on a plant fall within particular divisions, and to what extent these proportions are constant for different plants. Also, it is desirable to have definite information regarding the average length of the different axial divisions of the plant and the variation in this character. It is with these matters that the present section has to do.

Taking first the question of the proportion of the total number of whorls found on different parts of the plants, we have the results set forth in table 25. The figures in the vertical columns give the percentages which whorls borne on the specified part of the plant are of the total.

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TABLE 25.—*Proportionate numbers of whorls in different axial divisions of the plant.*

Series.	Plant.	Percentage of total whorls on—					
		(*a*) Main stem and divisions.	(*b*) Primary branches.	(*c*) Secondary branches.	(*d*) Tertiary branches.	(*e*) Quaternary branches.	Total number of whorls
I	1	30.7	59.2	10.1	.....	.....	228
	2	8.1	60.9	28.6	2.4	.....	161
	3	30.5	59.8	9.7	.....	.....	164
	4	12.2	65.4	22.0	.4	.....	263
	5	24.6	75.4	.....	.....	.....	61
II	1	10.2	58.8	28.8	2.2	.....	615
	2	13.4	69.3	17.3	.....	.....	313
III...	1	17.0	44.6	31.5	6.9	.....	523
IV	1	5.3	57.2	37.2	.3	.....	610
	2	5.4	50.4	42.3	1.9	.....	922
V	1	12.2	41.3	19.8	16.6	10.1	385
	2	87.5	12.5	.....	.....	.....	8
	3	45.5	54.5	.....	.....	.....	22
	4	30.8	69.2	.....	.....	.....	13
	5	50.0	50.0	.....	.....	.....	24
	6	23.0	77.0	.....	.....	.....	61
	7	20.4	51.0	19.0	4.8	4.8	147
VI	1	8.9	35.4	49.4	6.3	.....	79
	2	44.7	46.1	9.2	.....	.....	76
	3	34.8	65.2	.....	.....	.....	46
	4	48.9	56.1	.....	.....	.....	41
	5	19.0	46.3	24.1	10.6	.....	216
	6	17.4	61.4	21.2	.....	.....	236

These results are reasonably uniform, if, as is obviously fair, we leave out of consideration the very small plants, such as, for example, plants 2, 3, 4, and 5 of Series V. When the plant is so small as to have only a main stem and a few primary branches it is clear that the percentage of whorls on these two portions will not agree with what is found on large plants with many higher-order branches. Making due allowance for these irregularities, the results set forth in the table show that—

(*a*) In well-developed plants on the average more than half the total number of whorls are borne on primary branches. The actual weighted mean percentage given by the values in column (*b*) of the table is 54.7 per cent. As it is obviously unfair that a plant like No. 2 in Series V should have the same weight as No. 2 in Series IV, I have weighted each entry in determining this and the following means with the absolute size (i. e., in number of whorls) of the plant with which it is concerned.

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TABLE 26.—*Frequency distributions for size of primary branches.*

Whorls per branch.	Series I.						Series II.			Series III.	Series IV.		
	Plant 1.	Plant 2.	Plant 3.	Plant 4.	Plant 5.	Total.	Plant 1.	Plant 2.	Total.	Plant 1.	Plant 1.	Plant 2.	Total.
1	4	1	3	6	..	14	2	..	2	1	1	4	5
2	2	..	2	1	3	8	7	3	10	5	3	1	4
3	3	1	3	..	5	12	11	4	15	8	2	5	7
4	2	..	4	2	1	9	2	1	3	1	2	3	5
5	2	1	4	2	..	9	3	5	8	6	2	4	6
6	1	1	..	..	..	2	3	3	6	3	2	8	10
7	..	2	1	1	1	5	3	3	6	6	4	4	8
8	2	1	..	..	..	3	2	2	4	2	5	7	12
9	1	..	..	2	1	4	3	2	5	2	7	5	12
10	2	..	2	1	..	5	4	3	7	2	4	2	6
11	..	1	..	2	..	3	2	..	2	..	5	5	10
12	2	2	1	1	..	6	1	2	3	1	3	1	4
13	..	..	..	..	..	0	2	..	2	..	..	1	1
14	..	..	..	2	2	4	3	..	3	1	1	2	3
15	..	..	1	..	..	1	2	..	2	..	..	1	1
16	..	2	..	1	..	3	..	..	0	..	..	1	1
17	..	..	..	..	..	0	..	..	0	..	..	1	1
18	1	1	..	..	..	2	1	2	3	..	..	2	2
19	1	..	..	..	..	1	1	..	1	..	..	..	0
20	..	..	..	..	..	0	1	..	1	..	1	..	1
21	..	..	..	..	..	0	1	..	1	..	..	..	0
22	..	..	..	..	..	0	..	..	0	..	2	..	2
23	..	..	..	..	..	0	..	..	0	..	..	..	0
24	..	1	..	..	..	1	..	..	0	..	..	1	1
25	..	..	..	..	..	0	..	..	0	..	..	..	0
26	..	..	..	..	..	0	1	..	1	1	..	..	0
27	..	..	..	..	..	0	..	1	1	..	..	..	0
28	..	..	..	..	..	0	..	..	0	..	..	..	0
29	..	..	..	1	..	1	..	..	0	..	..	..	0
30	..	..	..	1	..	1	..	..	0	..	..	..	0
31	..	..	..	..	..	0	..	..	0	1	..	..	0
Total	23	14	21	23	18	94	55	31	86	40	44	58	102

Whorls per branch.	Series V.								Series VI.						
	Plant 1.	Plant 2.	Plant 3.	Plant 4.	Plant 5.	Plant 6.	Plant 7.	Total.	Plant 1.	Plant 2.	Plant 3.	Plant 4.	Plant 5.	Plant 6.	Total.
1	2	1	..	..	..	..	1	4	..	..	..	..	..	..	0
2	4	..	..	..	..	..	2	6	..	1	1	..	2	..	4
3	4	..	1	1	3	..	5	14	..	..	1	..	2	2	5
4	4	..	1	..	1	..	2	8	2	2	3	1	2	2	12
5	2	..	1	..	..	1	3	7	..	1	2	1	2	7	13
6	1	..	..	1	..	2	1	5	..	..	..	..	1	3	4
7	..	..	..	..	..	..	..	0	..	1	..	1	1	2	5
8	1	..	..	..	..	3	2	6	1	1	1	..	..	..	3
9	..	..	..	..	..	1	2	3	..	..	..	1	1	2	4
10	2	..	..	..	..	..	..	2	..	1	..	..	1	..	2
11	1	..	..	..	..	..	..	1	..	..	..	..	1	..	1
12	..	..	..	..	..	..	..	0	..	..	..	..	..	1	1
13	1	..	..	..	..	..	..	1	..	..	..	..	..	..	0
14	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
15	1	..	..	..	..	..	..	1	..	..	..	..	1	..	1
16	1	..	..	..	..	..	..	1	1	..	..	..	..	..	1
17	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
18	..	..	..	..	..	..	..	0	..	..	..	..	..	1	1
19	..	..	..	..	..	..	..	0	..	..	..	..	..	1	1
20	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
21	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
22	..	..	..	..	..	..	..	0	..	..	..	..	1	..	1
23	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
24	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
25	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
26	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
27	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
28	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
29	1	..	..	..	..	..	..	1	..	..	..	..	..	..	0
30	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
31	..	..	..	..	..	..	..	0	..	..	..	..	..	..	0
Total	25	1	3	2	4	7	18	60	4	7	8	4	15	21	59

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(*b*) Of the remaining whorls usually somewhat more are borne on secondary branches than on the main stem. This of course only applies to plants which have secondary branches. Taking all the plants together as they stand in the table, the weighted mean percentage contribution of the main stem to the total number of whorls is 14.1 per cent. Reckoned in the same way the mean percentage contribution of the secondary branches is 27.0 per cent, or very nearly twice that of the main stem.

(*c*) Tertiary and quaternary branches contribute, on the whole, a very small proportion of the total number of whorls. Calculating the mean percentage contribution from table 25, I find that it is 3.3 per cent for tertiary branches.

TABLE 27.—*Frequency distributions for size of secondary branches.*

Whorls per branch.	Series I.					Series II.			Series III.	Series IV.			Series V.			Series VI.				
	Plant 1.	Plant 2.	Plant 3.	Plant 4.	Total.	Plant 1.	Plant 2.	Total.	Plant 1.	Plant 1.	Plant 2.	Total.	Plant 1.	Plant 7.	Total.	Plant 1.	Plant 2.	Plant 5.	Plant 6.	Total.
1.....	5	1	4	5	15	5	4	9	12	6	3	9	9	..	9	..	..	..	..	0
2.....	8	..	4	5	17	8	8	16	10	8	6	14	4	1	5	..	..	1	..	1
3.....	2	2	2	3	9	8	3	11	2	8	6	14	1	..	1	2	2	1	..	5
4.....	2	1	..	..	3	5	1	6	4	5	12	17	6	2	8	2	1	3	3	9
5.....	1	..	..	2	3	5	2	7	3	7	4	11	1	1	2	1	..	1	2	4
6.....	..	1	..	3	4	4	..	4	2	6	5	11	1	1	2	1	..	4	1	6
7.....	..	1	..	1	2	4	..	4	2	4	3	7	1	..	1	1	..	..	1	2
8.....	..	..	..	..	0	2	1	3	1	2	3	5	1	..	1	..	..	..	2	2
9.....	..	..	..	..	0	1	..	1	3	2	4	6	1	..	1	1	..	..	..	1
10.....	..	1	..	..	1	..	..	0	2	1	2	3	..	1	1	..	..	..	..	0
11.....	..	..	..	..	0	..	..	0	1	1	1	2	..	..	0	..	..	..	..	0
12.....	..	..	..	..	0	..	..	0	1	..	2	2	..	..	0	..	..	1	..	1
13.....	..	..	..	..	0	1	..	1	0	1	1	2	..	..	0	..	..	..	..	0
14.....	..	..	..	..	0	..	..	0	0	1	2	3	..	..	0	..	..	..	..	0
15.....	..	..	..	..	0	..	..	0	0	..	1	1	..	..	0	..	..	..	..	0
16.....	..	1	..	..	1	..	..	0	0	..	2	2	..	..	0	..	..	..	..	0
17.....	..	..	..	..	0	..	..	0	0	..	1	1	..	..	0	..	..	..	..	0
18.....	..	..	..	..	0	..	..	0	0	..	1	1	..	..	0	..	..	..	..	0
19.....	..	..	..	..	0	..	..	0	0	..	1	1	..	..	0	..	..	..	..	0
Total..	18	8	10	19	55	48	19	62	43	52	60	112	25	6	31	8	3	11	9	31

The plants of Series IV differ in their percentage constitution very distinctly from the others, in the direction of having a lower proportion of main-stem whorls, and a higher proportion of secondary-branch whorls. The most striking exception in the table is afforded by plant 1 of Series VI, in which there are 14 per cent more whorls on secondary than on primary branches. But this is a small plant and clearly the probable errors of the percentages are high. As a matter of fact this plant had only three primary branches, while there were eight secondaries and one tertiary. It is not surprising, since the plant as a whole was so small, that the eight secondary branches should contribute a larger number of whorls to the total than the three primaries.

I wish to call attention at this point to a matter which otherwise might be overlooked. If the values given in table 25 be studied in connection with the constants given in table 2, it will be seen that there is

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in general marked agreement between the variation constants of plants which have similar percentage constitutions in respect to number of whorls. Thus, to take only a single example, we see from table 25 that plant 2 of Series I, and plant 1 of Series II, have very nearly the same percentage constitutions, although they are very different in *absolute* size. Table 2 shows that their variation constants are likewise in remarkably close agreement. This is of course what we should expect from our result that whorls on different portions of the plant form differentiated classes, and the fact that experience accords so closely with expectation is strong corroborative evidence, if any be needed, of the truth of our previous conclusions.

TABLE 28.—*Frequency distributions for size of tertiary branches.*

Whorls per branch.	Series I.			Series II.	Series III.	Series IV.			Series V.			Series VI.		
	Plant.		Total.	Plant 1	Plant 1	Plant.		Total.	Plant.		Total.	Plant.		Total.
	2	4				1	2		1	7		1	5	
1.....	3	1	4	3	2	1	3	4	1	..	1	..	..	0
2.....	..	..	0	4	2	1	2	3	..	..	0	..	..	0
3.....	..	..	0	2	1	..	3	3	1	1	2	..	..	0
4.....	..	..	0	0	0	..	1	1	3	1	4	..	2	2
5.....	..	..	0	0	3	..	..	0	1	..	1	1	2	3
6.	..	..	0	0	2	..	..	0	2	..	2	..	1	1
7.....	..	..	0	0	0	..	..	0	..	..	0	..	..	0
8.....	..	..	0	0	0	..	..	0	2	..	2	..	..	0
9-15.....	..	..	0	0	0	..	..	0	..	..	0	..	..	0
16.....	..	..	0	0	0	..	..	0	1	..	1	..	..	0
Total...	3	1	4	9	10	2	9	11	11	2	13	1	5	6

We may turn now to the question of variation in the size of the different axial divisions of the plant. In dealing with this phase of the subject, the number of whorls on any division of the plant will be taken as the measure of its size. For our present purpose this is a more satisfactory measure than absolute length would be. What we wish to determine is the *intra*-plant variability in respect to size of branch. In the analysis of the morphogenetic processes which will be taken up in a later section of the paper, it will be necessary to have some quantitative appreciation of how the branches of different orders compare in size, and what degree of variation in size they exhibit. We may turn at once to the data. The data respecting size of main stem have already been given in tables 5, 11, and 12. In table 26 (p. 50) is given for each plant, the frequency of primary branches of different sizes (i. e,, containing different numbers of whorls). In tables 27 (p. 51) and 28 are given in the same way the frequencies of secondary and tertiary branches of different sizes.

As was to be expected, the range of variation in the number of whorls to the branch is very large for the primary branches, and distinctly less

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for the secondaries. In order that a more definite idea may be obtained of the comparative distributions for the different orders of branches, I have prepared the diagrams given in fig. 9. These were made by plotting to the same base-unit the percentage frequencies of primary, secondary, and tertiary branches of different sizes, taking all the plants of Series I, II, and III together. In order to smooth out some of the irregularities in the distributions which arise from the relative smallness of our samples, I have doubled the size of the classes given in the tables.

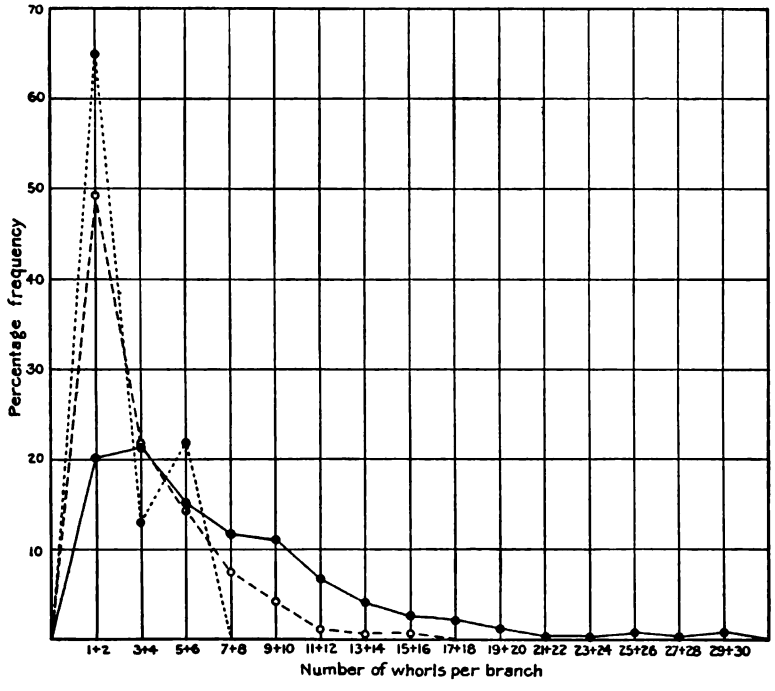

FIG. 9.—Frequency distributions for length of primary, secondary, and tertiary branches. The ordinates give percentage frequencies and the abscissas the number of whorls per branch. Primary branches, ●———— ; secondary branches, o– – – – ; tertiary branches, ●·····.

From these diagrams we see clearly the general nature of the variation in the size of branches. The smoothness of the primary and secondary branch curves is remarkable. The most frequently occurring branches, whatever their order, are those having from 1 to 4 whorls. The great range of secondary branches in length is rather surprising. As was to be expected, the proportionate number of branches with 1 or 2 whorls increases enormously as we pass from primary to tertiary branches. The diagrams show that the proportionate number of

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branches having from 3 to 6 whorls is approximately the same for primary, secondary, and tertiary branches.

In table 29 are given the constants for the variation in the size of primary and secondary branches for the totals of the series. On account of the relatively small numbers in most instances it is not worth while to give separately the values for each plant, nor for the tertiary branches.

TABLE 29.—*Constants for variation in size of primary and secondary branches.*

Series.	Order of branch.	Mean (unit — 1 whorl).	Standard deviation (unit—1 whorl)	Coefficient of variation
I	Primary	7.085±0.427	6.073±0.302	85.7
	Secondary	3.086± .238	2.621± .169	86.3
II	Primary	7.756± .411	5.657± .291	72.9
	Secondary	3.726± .208	2.424± .147	65.1
III	Primary	6.650± .622	5.829± .440	87.7
	Secondary	4.023± .335	3.253± .236	80.8
IV	Primary	8.324± .318	4.691± .222	56.4
	Secondary	5.857± .263	4.127± .186	70.5
V	Primary	5.567± .392	4.503± .277	80.9
	Secondary	3.548± .301	2.487± .213	70.1
VI	Primary	6.559± .367	4.175± .259	63.7
	Secondary	5.161± .252	2.081± .178	40.3

From this table we see that:

(*a*) There is surprisingly little difference between the different series in respect to mean size of branches.

(*b*) The mean size of primary branches is roughly twice that of secondaries.

(*c*) As was to be expected, the mean size of branches is the greatest in the series which was collected latest in the growing season (Series IV).

(*d*) Both absolutely and relatively to the mean size the variation is greater in primary than in secondary branches, with the single exception of Series IV, where, probably as a result of the great number and relatively large size of secondary branches, we get a higher proportionate variability in this group.

SUMMARY OF RESULTS.

Before taking up the discussion of the positional differentiation in detail, it is desirable to put together in a connected way the results which we have so far gained regarding the variation in leaf-number. By taking separately the whorls borne on different axial elements of the plant body we have found that there is a very sensible differentiation of whorls in respect to their leaf-number when they are grouped according to their general location on the plant. The nature of this

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differentiation is such that a progressive change occurs in the character of the variation constants as one passes from central to peripheral

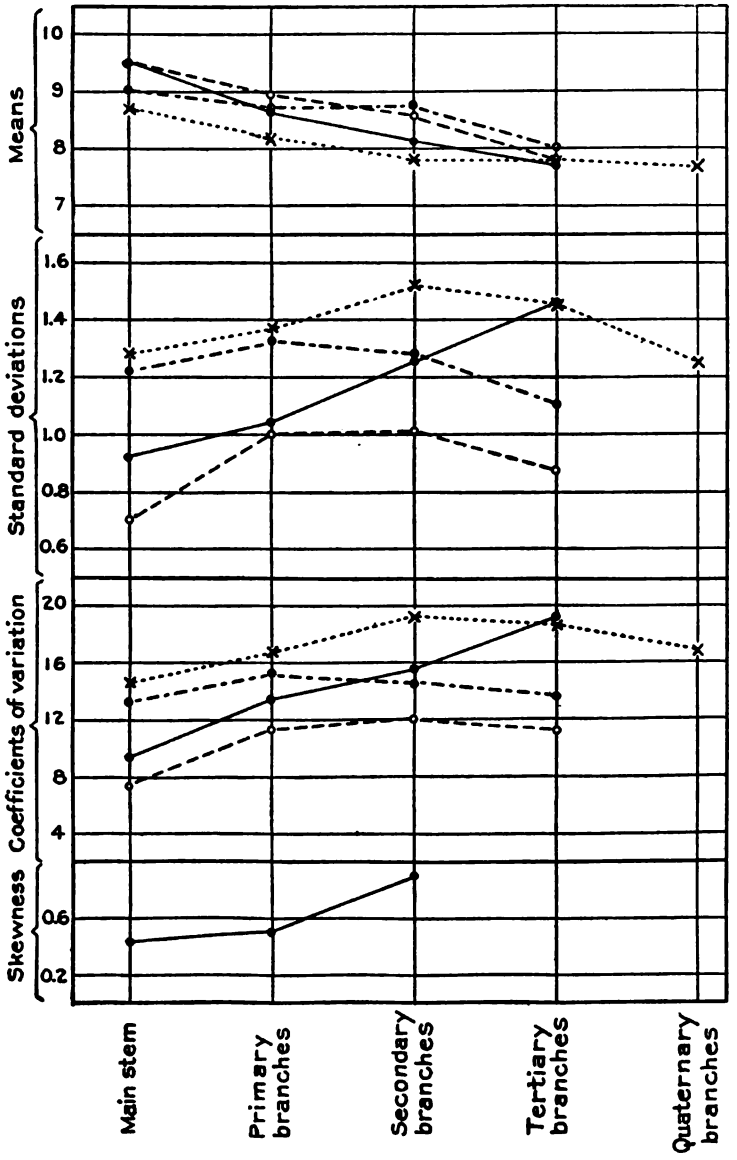

FIG. 10.—Diagram showing changes in the constants for variation in leaf-number in different portions of plant. Series I, II, and III combined ●——●; Series IV, ●– – –●; Series V, X·····X; Series VI, ●·····●.

portions of the plant until tertiary branches are reached. Here the order of events in part changes, and where previously certain of the

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constants had been increasing, they now begin to decrease, and *vice versa*. The nature of these changes in the character of the leaf-number variation in different portions of the plant may best be grasped as a whole from a graphical representation, such as is given in fig. 10. This diagram shows for four groups (viz, Series I, II, and III combined, Series IV, Series V, and Series VI) the changes as we pass from central to peripheral divisions in the following constants—mean, standard deviation, coefficient of variation, and skewness. The different constants are plotted to different vertical scales, which are in each case given at the side of the diagram.

This diagram makes plain at once the law which the variation in leaf-number in different sets of whorls follows. It may be stated in the following way: The mean number of leaves per whorl is highest in the whorls on the most central division of the plant (the main stem), and decreases regularly in the peripheral divisions. The whorls on the main stem are the least variable, and the variation increases regularly in the more peripheral divisions, till a maximum is reached in secondary-branch whorls. The variation then tends to diminish in the whorls on higher-order branches. Now, from the method of growth of Ceratophyllum, it is clear that as a class the main-stem whorls are the oldest, the primary-branch whorls as a class stand next in age, secondary and tertiary branch whorls next, while quaternary-branch whorls will on the whole be youngest. Of course these distinctions are not absolute for every whorl; there may, for example, be individual whorls on the main stem which are younger than individual whorls on any branch, but on the average it is evident that the more peripheral parts will be the younger. So, then, we find that as a general rule *the older the portion of the plant the greater will be the average number of leaves to the whorl. Further, the variation in leaf-number is least in the oldest portion of the plant and increases in the younger portions, but reaches a maximum one or two divisions short of the youngest.*

Besides the changes in type and variability, there are marked differences in other respects between whorls in different parts of the plant. Thus for example, the skewness appears to be greater in the variation of whorls on the younger portions of the plant, though on account of paucity of material we can not go farther than secondary branches, with the analytical constants.

It is perfectly clear from the results which have been presented that in a general way at least the number of leaves in a whorl and the position of the whorl on the plant are related. But how close is the relation? Does it hold within an axial division (say primary branches) that the

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size of the whorl is a function of its position on the axis? So far we have demonstrated positional differentiation of broad classes of whorls. It now remains to determine whether this extends to the individual whorls, and in general to find out the laws of growth which result in main-stem or primary-branch, or secondary-branch, or other whorls, showing the particular characteristics in their variation which they do. Cases of positional differentiation in like parts are well known in a number of plants,[1] but a complete analysis of the phenomenon which takes into account the whole series of repeated parts or characters for a large and richly branching plant like Ceratophyllum has not hitherto been undertaken.

THE RELATION BETWEEN THE NUMBER OF LEAVES IN THE WHORL AND POSITION ON THE PLANT.

We come now to the more direct investigation of the morphogenetic laws concerned in the formation of the leaf-whorls. From the method of growth in lateral branches of Ceratophyllum it is clear that we have an almost ideal form for such a study. The whorls on a branch present a linear series of parts in which we know the order of formation in time (cf. p. 10, *supra*). Such a system suggests at once a number of very interesting problems in morphogenesis. It will conduce to clearness, if we base the discussion of our results on such individual problems, taking up the different ones in order.

POSITION REGRESSION IN DIFFERENT PORTIONS OF THE PLANT—THE FIRST LAW OF GROWTH IN CERATOPHYLLUM.

The first problem which logically presents itself may be stated in this way: In a series of like parts produced in a regular ordinal succession what relation exists between the form of a particular member of the series and its ordinal position? If there is a change in the character of successively formed parts, what law governs this change? It is obvious that this problem is a very fundamental one, because of the fact that one of the most frequently occurring plans of structure which we know in the organic world is the metameric. In this type of structure the organism is built up of a series of primitively similar units arranged in linear order. Our problem is to find out, if possible, in a very simple case the laws of differentiation in such a system. The biometrical solu-

[1]Many examples are given by Miss Tammes (:03) and the subject has been investigated biometrically by Pearson (:05) in *Asperula odorata* and *Equisetum arvense* and by Pearson and Radford (:04) in beech leaves.

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tion of the problem is theoretically clear. What we want to know are the correlations and regressions between any character of the members of such linear series and their position. In this particular case we have to determine the correlation and regression between the number of leaves in the whorl and position.

It is evident that the different axial divisions of the plant must be treated separately. Logically the main stem should be considered first, but for reasons which will appear as we go on, it is desirable to take up the primary and secondary branches before the main stem. The correlation tables showing for each series the relation between number of leaves in the whorl and position on primary branches follow. In the case of Series V and VI the tables have been cut off at the tenth whorl because the very small number of entries beyond that point did not make it worth while to keep them. In the other four series every possible whorl has been included. Furthermore, the tables for Series V and VI differ from the others in that in these two series all branches (primary, secondary, tertiary, etc.) have been clubbed together. Otherwise the numbers would have been too small to get any results at all for these series. No confusion need result from this procedure, as the whole discussion of positional differentiation will be based on the first four series, the last two (V and VI) being used merely to illustrate and confirm the conclusions reached from the others. The method of designating position has been fully explained and illustrated in an earlier section of the paper (p. 12 and fig. 2, *supra*) and need not be repeated here in detail. It is merely necessary to recall that the whorls are numbered in order, beginning at the proximal end of the branch; the "first whorl" (1) thus being in the case of a primary branch the whorl nearest the main stem, in the case of a secondary branch the whorl nearest the primary, etc.

Mere inspection of these tables shows us at once that the character of the whorls in respect to leaf-number changes as we go out on the branch. It is perfectly clear in a general way that the farther a primary-branch whorl is from the main stem, the more leaves it is likely to have. Or, in other words, we see that there is a clear positional differentiation *within* an axial division of the plant. The character of successively formed parts changes with the order of their formation. We may at once proceed, then, to the analysis of the laws of this change. As a first step it is necessary to know the exact degree of the correlation between leaf-number and position, and to test whether the regression is linear or not. The test for linearity of regression has been given by Pearson (:05). It consists in determining for any system of correlated

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TABLE 30.—*Correlation between leaf-number and position of primary-branch whorls.*

SERIES I.

Number of leaves per whorl.	Position of whorl on branch.																											Total.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
5	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
6	21	5	1	1	1	1	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	32
7	21	16	7	6	3	1	1	2	1	1	1	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	62
8	19	26	26	17	15	7	9	2	6	1	3	4	1	1	..	..	..	1	..	1	..	..	..	..	..	..	1	1	..	..	141
9	6	16	22	18	9	17	13	12	10	12	8	4	3	3	3	3	2	2	1	..	1	1	..	1	..	..	..	..	..	..	177
10	..	1	2	8	4	7	7	11	9	11	9	6	7	9	8	4	4	2	3	2	1	2	3	..	1	1	1	1	1	..	125
11	..	..	..	..	..	1	1	1	2	..	..	1	1	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..	..	..	9
Total	70	64	58	50	42	34	32	28	28	26	21	15	13	13	11	8	6	5	4	3	3	3	3	2	0	2	2	1	1	1	549

SERIES II.

Number of leaves per whorl.	Position of whorl on branch.																											Total.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
5	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
6	19	2	1	..	2	..	..	..	..	2	1	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	29
7	35	18	7	4	3	..	1	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	71
8	12	25	25	20	6	10	6	5	4	3	..	2	2	1	..	..	1	1	1	2	..	..	..	..	..	..	..	..	..	..	126
9	4	19	25	24	28	22	18	10	7	6	1	3	2	1	2	1	1	1	1	..	2	..	..	..	..	..	..	..	..	..	178
10	..	4	5	5	11	9	13	14	17	12	13	8	7	9	7	6	5	4	2	2	3	..	2	1	2	2	1	1	..	..	165
11	..	..	2	..	1	..	1	..	..	1	..	2	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	8
Total	70	69	65	53	51	41	39	30	30	24	15	16	11	11	9	7	7	7	4	4	3	2	2	2	2	2	1	1	..	..	578

SERIES III.

Number of leaves per whorl.	Position of whorl on branch.																											Total.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
6	12	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	13
7	10	8	2	1	1	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	25
8	12	15	8	10	6	2	3	2	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	59
9	..	9	15	10	13	9	6	5	2	1	1	1	1	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	76
10	..	1	4	3	3	3	3	2	3	3	3	2	2	2	2	1	1	1	2	2	2	2	2	2	2	2	1	1	1	1	59
11	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Total	34	34	29	24	23	14	12	10	7	4	4	4	3	3	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	233

SERIES IV.

Number of leaves per whorl.	Position of whorl on branch.																											Total.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
3	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0
5	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
6	9	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	10
7	41	8	4	2	5	3	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	65
8	33	41	25	14	7	5	3	5	4	1	3	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	..	144
9	8	38	51	51	38	37	35	18	11	10	7	3	4	3	1	2	1	2	1	1	..	1	..	..	..	..	..	..	..	..	323
10	1	6	8	15	27	26	25	32	24	21	14	12	10	9	9	7	6	4	3	2	2	1	1	1	..	..	..	..	..	..	266
11	..	1	..	1	..	..	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
Total	93	95	88	83	77	71	64	55	40	33	25	16	14	12	10	10	9	6	4	3	2	2	1	1	..	..	..	..	..	..	814

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variables a constant, η, called the *correlation ratio*, and defined by the expression

$$\eta = \frac{\sigma_{m_y}}{\sigma_y}$$

In other words, the correlation ratio is the ratio of the variability of the means of the arrays of one correlated character to the total variability of that character, as exhibited by the sample as a whole. The constant η has the same value as the coefficient of correlation r only when the regression is perfectly linear. If the regression is not linear η will be greater than r. Then evidently $\eta \sim r$ is a measure of the approach of the regression to linearity. Recently Blakeman (:05) has given methods of obtaining the probable error of various functions of $\eta \sim r$.

TABLE 31.—*Correlation between leaf-number and position. Whorls on all branches.*

Number of leaves per whorl.	Position of whorl on branch—Series V.										
	1	2	3	4	5	6	7	8	9	10	Total.
4	2	2	..	..	..	..	..	..	..	..	4
5	17	5	1	2	..	1	1	..	..	..	27
6	16	6	10	1	1	1	..	1	..	..	36
7	40	29	18	14	9	1	2	4	1	..	118
8	19	28	25	17	8	7	3	..	3	1	111
9	5	20	19	26	22	17	13	6	4	5	137
10	7	5	6	4	6	10	8	14	4	3	67
11	1	..	..	..	..	..	..	..	..	..	1
Total	107	95	79	64	46	37	27	25	12	9	501

Number of leaves per whorl.	Position of whorl on branch—Series VI.										
	1	2	3	4	5	6	7	8	9	10	Total.
5	7	..	..	1	..	..	..	1	..	..	9
6	19	4	..	..	..	..	..	..	..	..	23
7	37	16	3	4	2	1	1	1	..	1	66
8	20	33	24	12	8	6	1	..	1	..	105
9	6	26	30	32	11	6	5	3	2	2	123
10	5	12	29	25	31	19	16	9	10	4	160
11	..	..	1	1	..	1	1	1	1	..	6
Total	94	91	87	75	52	33	24	15	14	7	492

TABLE 32.—*Correlation between leaf-number and position. Whorls on primary branches. Series I, II, and III combined.*

Number of leaves per whorl.	Position of whorl on branch.																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total.
5	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
6	52	8	2	1	3	1	1	..	..	3	1	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	74
7	66	42	16	11	7	1	2	4	5	1	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	158
8	43	66	59	47	27	19	18	9	10	4	3	6	3	2	..	..	2	2	1	3	..	..	..	..	..	1	1	..	..	..	326
9	10	44	62	52	60	48	37	27	19	19	10	8	6	5	5	5	3	4	2	..	1	3	..	1	..	..	..	..	..	..	431
10	..	6	11	16	18	19	23	27	29	26	25	16	16	20	17	11	10	7	7	6	6	4	7	3	4	5	3	3	2	2	349
11	..	..	2	..	1	1	2	1	2	1	..	4	1	..	..	..	..	..	..	..	1	..	..	2	..	..	..	..	..	..	18
Total	174	167	152	127	116	89	83	68	65	54	40	35	27	27	22	17	15	14	10	9	8	7	7	6	4	6	4	3	2	2	1,360

In table 33 are given the values of r and η with their probable errors deduced from the data given in tables 30 to 32. The probable errors of r tabulated were computed from the formula

$$\text{Probable error of } \eta = \pm 0.67449 \frac{(1-\eta^2)}{\sqrt{N}}$$

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Pearson (*loc. cit.*) has shown that this expression is sufficiently accurate for all ordinary purposes, and it is much easier to calculate than the complete expression for the standard deviation of η.

TABLE 33.—*Correlation between leaf-number and position of primary-branch whorls.*

Series.	Coefficient of correlation. r	Correlation ratio. η	Table.
I	0.540±0.020	0.655±0.017	30
II	.522± .020	.652± .016	30
III	.597± .028	.760± .019	30
IV	.521± .017	.657± .013	30
I, II, and III combined	.540± .013	.667± .010	32
V (all branches)	.475± .023	.494± .023	31
VI (all branches)	.528± .022	.636± .018	31

We see at once from table 33 that—

(1) There is a very considerable degree of correlation between the number of leaves per whorl and the position of the whorl.

(2) The degree of correlation is very closely the same for all series. We should expect, of course, that Series V and VI would give different values for the coefficients, because in those cases we are dealing with three and four different orders of branches together.

(3) There can be no doubt that the regressions are not linear. The differences between η and r are so considerable that I have not thought it necessary to work out the probable errors for every case. The series which gives the smallest difference between r and η is V ($\eta - r = 0.0197$), but the apparent approach to linearity here is due to putting different orders of branches together. Considering the primary branches alone, the minimum difference between η and r is given by Series I ($\eta - r = 0.1142$). We may take these two instances as a sample:

It has been shown by Blakeman (*loc. cit.*) that if we let

$$\zeta = \eta^2 - r^2$$

an approximate formula for the probable error of ζ, i. e., E_ζ, is

$$\frac{\zeta}{E_\zeta} = \frac{\sqrt{N}}{0.67449} \cdot \tfrac{1}{2}\sqrt{\zeta}\,\frac{1}{\sqrt{1+(1-\eta^2)^2-(1-r^2)^2}}$$

Working from this formula we have for Series I,

$$\zeta = 0.1364 \pm 0.0193,$$

and for Series V,

$$\zeta = 0.0191 \pm 0.0082.$$

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In the first case the constant is, of course, certainly significant in comparison with its probable error, and in the second case very probably significant.

It thus being clear that the relation between leaf-number and position of whorl is not a simple linear one, it becomes necessary to find out what it is. To do this we must first see what the exact form of the observed regression is. In table 34 is given the mean leaf-number for each array of whorls occurring in a given position, as indicated in tables 30 to 32.

TABLE 34.—*Mean number of leaves in successive whorls on primary branches.*

Position of whorl.	Mean number of leaves.						
	Series I.	Series II.	Series III.	Series IV.	Series I, II, and III combined	Series V.[a]	Series VI.[a]
1	7.057	7.014	7.000	7.441	7.029	6.981	7.149
2	7.875	8.043	8.029	8.453	7.970	7.642	8.286
3	8.293	8.492	8.724	8.685	8.461	7.873	9.011
4	8.520	8.566	8.625	8.988	8.559	8.188	9.040
5	8.524	8.902	8.783	9.130	8.741	8.500	9.365
6	8.912	8.976	9.071	9.211	8.966	8.838	9.394
7	8.844	9.179	9.000	9.313	9.024	8.889	9.625
8	9.250	9.233	8.800	9.491	9.176	9.120	9.333
9	9.179	9.300	8.857	9.550	9.200	8.916	9.786
10	9.192	9.208	9.750	9.438	9.241	9.222	9.286
11	9.300	9.000	9.750	9.360	9.425	.....	.....
12	9.267	9.438	10.000	9.875	9.429	.....	.....
13	9.462	9.455	9.667	9.714	9.481	.....	.....
14	9.615	9.727	9.667	9.750	9.667	.....	.....
15	9.727	9.778	10.000	9.900	9.773	.....	.....
16	9.250	9.857	9.500	9.600	9.529	.....	.....
17	9.667	9.571	9.000	9.444	9.533	.....	.....
18	9.200	9.000	9.500	9.667	9.143	.....	.....
19	9.750	9.250	10.000	9.750	9.600	.....	.....
20	9.333	9.000	10.000	9.667	9.333	.....	.....
21	10.000	10.000	10.000	10.000	10.000	.....	.....
22	9.667	9.000	10.000	9.500	9.571	.....	.....
23	10.000	10.000	10.000	10.000	10.000	.....	.....
24	10.000	10.500	10.000	10.000	10.167	.....	.....
25	.....	10.000	10.000	.....	10.000	.....	.....
26	9.000	10.000	10.000	.....	9.667	.....	.....
27	9.000	10.000	10.000	.....	9.500	.....	.....
28	10.000	10.000	10.000	.....	10.000	.....	.....
29	10.000	.....	10.000	.....	10.000	.....	.....
30	10.000	.....	10.000	.....	10.000	.....	.....

[a] It will be remembered that in these two series all branches are clubbed together, while in the case of the other series we are dealing here with primary-branch whorls only.

There is no doubt from the figures in this table that the form of the regression line is essentially the same for all the series. In order to show this graphically I have prepared fig. 11, in which the observed regression lines for Series I, II, III, and IV are plotted. To prevent con-

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fusion Series V and VI have not been included, but examination of the values in table 34 is sufficient to show that they are not essentially different from the others. In the diagrams the ordinates give the means as recorded in table 34 and the abscissas the position of the whorls.

These diagrams at once make clear the following points:

(*a*) The regression is evidently not linear. Starting with a low value for the first whorls, the curves all show a sharp rise, amounting to almost exactly one leaf, to the second whorl. From the second to the third whorl there is approximately half as great a rise as from the first to the second. From the third whorl on, while the general trend of the lines is upward, their slope becomes more and more gradual. The maximum towards which the lines tend is clearly 10-leaved whorls, though on account of the small number of entries in the outlying parts of the correlation tables at the upper end, the regression lines become very irregular on these high values.

(*b*) While the form of the regression line is clearly the same in Series IV as it is in Series I, II, and III, it differs in being practically uniformly higher. It starts nearly a half leaf higher on the first whorl, and maintains this difference on the whole very evenly out to the 15th whorl. From that point it becomes more irregular on account of the paucity of observations.

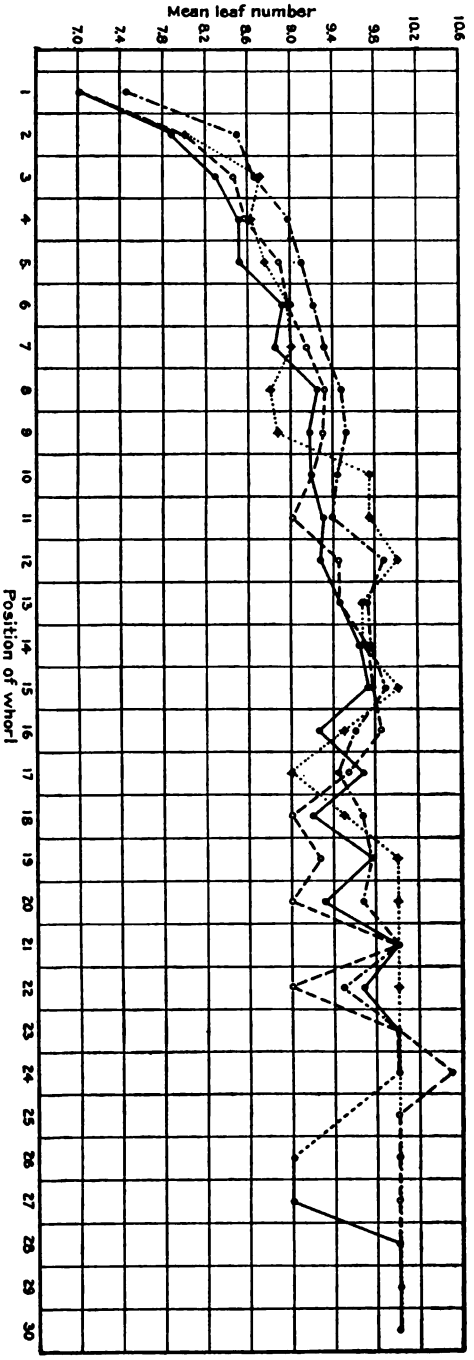

FIG. 11.—Regression line, showing change of mean leaf-number with position. Primary branches. Series I, ●——●; Series II, ○– – –○; Series III, ◆·····◆; Series IV, ●–·–·–·–●.

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(*c*) There is evidently a definite functional relation (in the mathematical sense) between the number of leaves in a whorl and its position. Biologically this means that the form of a particular whorl is in some manner related to the number of whorls which the growing bud has previously formed. Successively formed whorls show an increase in the number of leaves.

The values in table 34 and the diagrams indicate that this increase follows a definite law. We can in general formulate this by mere inspection of the data. There is an *increase* in the mean number of leaves in successively formed whorls, but the increment in leaf-number *diminishes* with each successive whorl. So much is clear, but we are only thrown back to the discovery of the law according to which the increment diminishes. So far as I can see, any kind of biological reasoning is powerless to help us further. Observation shows that there is some sort of a functional relation between number of leaves in the whorl and position, just as observation indicates to the physicist that there is a functional relation between two things. But to determine the nature of the functional relation, or in other words, to find out the law which the phenomena follow, we are compelled, so far as I can see, to resort to mathematical treatment of the data. The physicist has done this, of course, for a very long time. If this is a logical, scientific method in physics (and I presume no biologist has any doubt that it is), why is it not equally logical and scientific when a precisely similar problem is presented by biological phenomena?

To formulate the law of growth according to which the change in mean leaf-number in the successively formed whorls of a Ceratophyllum plant occurs we must turn to mathematics, as biological reasoning will not help us further. I have dwelt at some length on this point in order to show that in one particular class of biological problems at least we are compelled to call mathematics to our aid, or else to be content to stop considerably short of a goal within easy reach. The idea seems to prevail among many biologists that the application of higher mathematical methods to biology is altogether idle and futile. It seems possible that something may be done towards removing this unfortunate prejudice if clear and definite statements telling just why it is necessary to resort to mathematics if we are to advance on particular problems, are more frequently made in biometrical writings.

The mathematical problem before us is this: If we let y indicate the mean number of leaves per whorl and x the position of the whorl on a primary branch, then direct observation shows us that

$$y = \phi(x).$$

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We have to determine the form of the function ϕ. It is obvious that the proper way to set about this is to find out what curve best graduates the observed data, and the equation to this curve will be the expression of the law of growth which we are seeking. While the problem is thus theoretically a simple one, practically it is an extremely difficult one, because if the data give no clue at the start as to what the nature of $\phi(x)$ is, which unfortunately is usually the case, we have to resort to a very laborious process of trial and error. Different curves must be fitted one after another to the data until the right one is found. It is the usual custom among physicists to assume a parabola and get the best fit possible by increasing the number of constants. This method is not, however, a theoretically justifiable one, because, as Pearson (:02, p.19) has pointed out:

> There are often considerations, lying outside the actual data, which suffice to indicate that trigonometrical, exponential, or other types of curves will give better results than parabolas. A parabola which passes even through all the observations may indeed be a most undesirable representation of the facts, for it has twisted and curled to account for error as well as to give the general sweep of the observations.

The figures in table 34 and the diagrams in fig. 11 show clearly that the nature of the regression curve is the same for all the series, and that further, the absolute values for Series I, II, and III are, within the limits of error from random sampling, identical. Hence on account of the very laborious character of the arithmetic involved, these three series (I, II, and III) were combined, and in what follows this combined material will serve as a basis. By this proceeding a considerable gain in smoothness of the figures to work from was made, without any loss of accuracy. The means for the combined series are given in the fifth column of table 34.

Having at the outstart no idea of the nature of $\phi(x)$, it was decided as a beginning to fit a series of parabolas to these data. That is to say, in the expression

$$y = \phi(x)$$

it was assumed that

$$\phi(x) = c_0 + c_1x + c_2x^2 + c_3x^3 + \ldots c_nx^n.$$

By taking more and more terms of this expansion we get successively higher order parabolas. There is no theoretical limit to the process, but obviously, if we are seeking a true graduation formula, it is idle to go higher than the sixth-order term, for the reason mentioned above. Furthermore, to get the sixth-order parabola, we require moments up to and including the sixth, and as Pearson (:05 and elsewhere) has shown, the probable errors of the higher moments rapidly

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become very large indeed. Each entry in column 5 of table 34 was taken as the ordinate (y) at a given position (x). As there was no apparent biological reason for weighting differently the whorls in different positions, all whorls were given equal weight. The method of fitting was that of moments given by Pearson (:02). Since it is necessary in this method to have an odd number of whorls, the first 29 were dealt with instead of the whole 30. The origin was taken at $x = 15$. The observations were considered to give a system of trapezia, and the proper corrective terms for the moments of such a system as given by Pearson (:02, p. 8) were used. The range is from 1 to 29, or we have

$$2l = 28, \text{ or } l = 14.$$

For the quantities $\lambda_s = \frac{\mu'_s}{l^s}$, where μ'_s is the sth moment about the origin and l is half the total range, the following values were obtained,

$$\lambda_1 = 0.030132 \qquad \lambda_4 = 0.193246$$
$$\lambda_2 = .326446 \qquad \lambda_5 = .015303$$
$$\lambda_3 = .020219 \qquad \lambda_6 = .136507$$

Further, we have

$$y_0 = 9.3454.$$

From these values the following series of parabolas was obtained, in which x is measured from the mid-range (= 15).

(I) $$y = 9.3454\left\{1 + 0.090397\left(\frac{x}{l}\right)\right\}$$

(II) $$y = 9.3454\left\{1.025828 + 0.090397\left(\frac{x}{l}\right) - 0.077483\left(\frac{x}{l}\right)^2\right\}$$

(III) $$y = 9.3454\left\{1.025828 + 0.034226\left(\frac{x}{l}\right) - 0.077483\left(\frac{x}{l}\right)^2 + 0.093608\left(\frac{x}{l}\right)^3\right\}$$

(IV) $$y = 9.3454\left\{1.013268 + 0.034226\left(\frac{x}{l}\right) + 0.048110\left(\frac{x}{l}\right)^2 + 0.093608\left(\frac{x}{l}\right)^3 - 0.146524\left(\frac{x}{l}\right)^4\right\}$$

(V) $$y = 9.3454\left\{1.013268 + 0.036131\left(\frac{x}{l}\right) + 0.048110\left(\frac{x}{l}\right)^2 + 0.084725\left(\frac{x}{l}\right)^3 - 0.146254\left(\frac{x}{l}\right)^4 + 0.008002\left(\frac{x}{l}\right)^5\right\}$$

(VI) $$y = 9.3454\left\{1.029148 + 0.036131\left(\frac{x}{l}\right) + 0.285372\left(\frac{x}{l}\right)^2 + 0.084725\left(\frac{x}{l}\right)^3 + 0.853919\left(\frac{x}{l}\right)^4 + 0.008002\left(\frac{x}{l}\right)^5 - 0.783659\left(\frac{x}{l}\right)^6\right\}$$

In order to show the nature of the results with these parabolas fig. 11 *bis* has been prepared. This gives the observations and three of the higher-order parabolas (namely, the third, fifth, and sixth). It

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seemed hardly worth while to plot the lower-order curves, because if the higher ones fail to represent the data, it is reasonably certain that the lower will, and further, six superimposed curves on the same data tend to make a rather confused diagram. As will be seen from equations IV and V above, the fourth and fifth order curves are sensibly identical, and hence it is unnecessary to plot both of them.

Examining these curves, we see that they signally fail to give as good a result as we want and have reason to expect. The third and fifth order curves do not give at all the form of the curve at the lower end of the range. This is clearly the most important part of the curve and a failure to give a good graduation here is fatal and at once throws out of court the lower-order curves. The sixth-order curve does somewhat better, especially at the start of the range, but it is evident that the fit is a purely artificial one and does not help us any towards the law of growth we are seeking. In the first place, this curve has altogether too many points of inflexion to correspond to the biological facts. It is, in a word, fitting itself to the "errors" rather than to the general sweep of the observations. The artificial character of the graduation is well brought out at the upper end of the range, where the curve takes a very sharp and sudden turn downward, corresponding to nothing in the observations. We may be quite sure that the correct expression

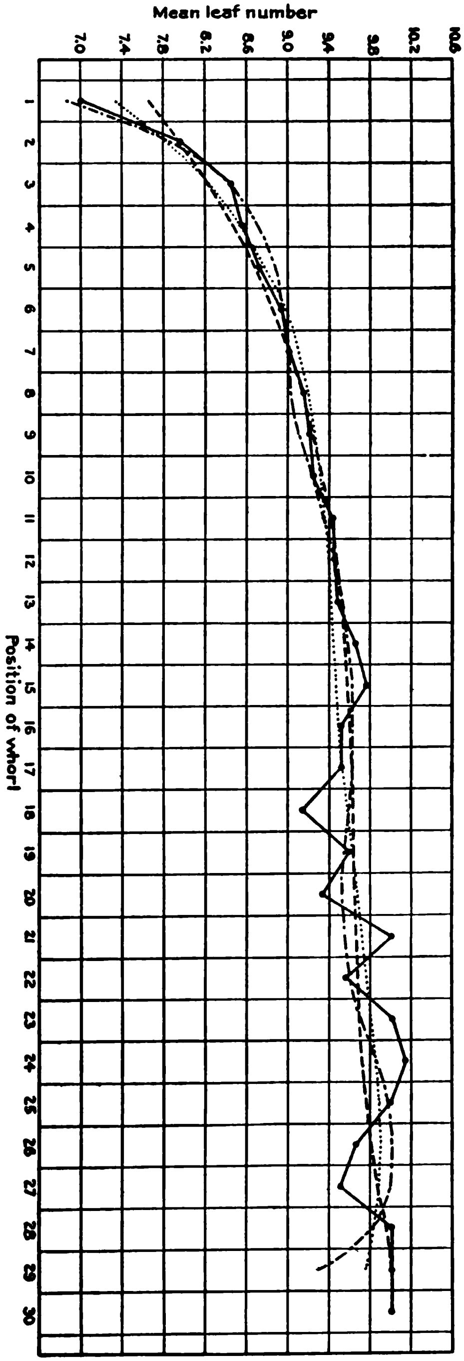

FIG. 11 *bis*.—Regression line and fitted parabolas, showing change of mean leaf-number with position. Primary branches, Series I, II, and III combined. Observations, •——— ; third order parabola, — — — — — ; fifth-order parabola, ... ; sixth-order parabola, —·—·—·—.

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for the law of growth here will be such a one that it will give reasonable results for extrapolation at the upper end of the range. That is to say, the same curve which gives a good graduation for the first 29 whorls, ought, if it is to have any biological validity, to give a reasonable result when extended to the 30th and further whorls. It is clear that none of these parabolas is at all satisfactory in this respect. The general failure of parabolas to give good extrapolation results, though they may be entirely satisfactory for interpolation, has been recently emphasized by Miss Perrin (:04). The results obtained in the present case form an excellent confirmation of her general position. On the whole these results show very clearly that to put

$$\phi(x) = c_0 + c_1x + c_2x^2 + c_3x^3 \ldots . \quad c_nx^n$$

is inadequate in the present case. The form of the function which expresses the true relation between size of whorl and its position is something different from this.

As has been mentioned above, inspection of the regression lines shows that while the mean number of leaves per whorl increases the farther out we go on the branch, yet at the same time the increment at each successive whorl diminishes. This at once suggests another hypothesis regarding the function. If we let dy denote a small change in mean leaf-number and dx a small change in position, we may assume that

$$\frac{dy}{dx} = \frac{1}{x} \text{ . const.}$$

or in other words that the *rate* of increase in mean leaf-number varies inversely as the position on the axis. This leads at once to a logarithmic curve, which may be put in the following form.

$$y = A + C \log x,$$

where A and C are constants to be determined from the data, and, as before, y and x measure respectively leaf-number per whorl and position. In order to test the worth of our assumption it was decided to try fitting a curve of this type.

The same data as before were used. Before beginning the actual calculation of the constants for the fitting, however, a graphical "first smooth" of the observations given in column 5 of table 34 was made on a large scale and the smoothed ordinates read off. The values so obtained furnished the raw material for the actual fitting. As before, all the ordinates were given equal weight. Since we may obviously take the origin of y (i. e., of the ordinates) anywhere we please, it was for practical reasons taken at 7 leaves. So that in the actual work each

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ordinate was expressed as a deviation (in excess or defect) from 7. The origin of x was taken at 0, i.e., at the proximal end of the branch. A curve of the type

$$y = A + C \ (\log x)$$

was then fitted by the method of least squares.

It gave on the whole a very good graduation; so good as to indicate clearly that one was on the right track. It signally failed, however, to give a good result at the lower end of the range. It bent altogether too gradually at the start to represent the facts. Weighting the ordinates with their observed frequencies did not help matters at all. While in this way a better fit at the start of the range was obtained, it was at the expense of getting very improbable values for whorls beyond the 10th or 12th. The results clearly showed, however, that some logarithmic curve offered the solution of the problem. It only remained to find the proper logarithmic curve.

The next assumption to be tested was that the true law of growth was such that

$$\frac{dy}{dx} = \frac{1}{x-a} \text{ const.}$$

or, in other words, that the rate of increase in mean leaf-number varied inversely *as the position measured from a fixed point* (a) *on the axis.* This leads to a curve of the form

$$y = A + C \log (x - a).$$

In fitting this curve a value of 0.8 for the constant a was first found by a rough method of approximation. Then putting this value of 0.8 for a into the equation, the constants A and C were found by the method of least squares. This gave a first approximation to the curve. The next step was to proceed to get a better fit by modifying all the constants by small amounts, the modifying terms being calculated by the method of least squares. The final equation determined was

$$y = 0.9520 + 1.3608 \log (x - 0.8015)$$

Remembering that y has been measured from 7, we have for the final result

$$Y = 7.9520 + 1.3608 \log (x - 0.8015) \quad . \quad . \quad . \quad . \quad \text{I}$$

where Y denotes the actual mean number of leaves per whorl and x the position of the whorl. Calculating the ordinates of this curve corresponding to the successive ordinal positions of the whorls, we have the series of values given in the second column of table 35, against which are put for comparison the actually observed values.

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The graduation is clearly a remarkably good one. A mean error of 0.0004 between observation and theory, when we are dealing with 30 ordinates is clearly as low as we could expect to get, considering the probable errors to which the individual observations are subject. There can be no doubt that we have found the mathematical expression of the law according to which growth in the character under consideration takes place.

TABLE 35.—*Comparison of observed and calculated mean leaf-number for successive whorls of primary branches. Series I, II, and III combined. Logarithmic curve.*

Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.	Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.
1	7.029	7.004	+0.025	16	9.529	9.560	— .031
2	7.970	8.059	— .089	17	9.533	9.600	— .067
3	8.461	8.418	+ .043	18	9.143	9.633	— 490
4	8.559	8.639	— .080	19	9.600	9.667	— .067
5	8.741	8.800	— .059	20	9.333	9.698	— .365
6	8.966	8.926	+ .040	21	10.000	9.728	+ .272
7	9.024	9.030	— .006	22	9.571	9.757	— .186
8	9.176	9.119	+ .057	23	10.000	9.784	+ .216
9	9.200	9.195	+ .005	24	10.167	9.810	+ .357
10	9.241	9.264	— .023	25	10.000	9.835	+ .165
11	9.425	9.324	+ .101	26	9.667	9.859	— .192
12	9.429	9.380	+ .049	27	9.500	9.882	— .382
13	9.481	9.430	+ .051	28	10.000	9.904	+ .096
14	9.667	9.477	+ .190	29	10.000	9.926	+ .074
15	9.773	9.520	+ .253	30	10.000	9.946	+ .054
Sum of deviations							+ .011
Average deviation per observation							+ .00037

The curve and the observations are shown in plate I.

This result I believe to be of very considerable interest and significance from several points of view. In the first place, it gives us a precise and unique formulation of a fundamental law of growth and differentiation in Ceratophyllum. We now know the nature of the change in successively formed whorls on the growing branch. Before proceeding to state this law in words it should be remembered that the differential coefficient of our equation is

$$\frac{dy}{dx} = \frac{1}{x-a} \cdot \text{const.}$$

where the constant is, of course,

$$\frac{C}{\log_e 10}.$$

Or the law of change in successively formed whorls on primary branches in Ceratophyllum may be stated in the following way: *The mean num-*

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ber of leaves per whorl increases with each successive whorl, and in such a way that not only does the absolute increment diminish, but also the rate of increase diminishes, as the ordinal number of the whorl measured from a fixed point increases. Or, put more briefly, the rate of increase in leaf-number at any given point as we go out on the branch varies inversely as the number of whorls which separate the given point from a fixed point, the a of our equation.

As a consequence of the fact that the rate of increase in leaf-number constantly diminishes as we go out on the branch, it is evident that the actual number of leaves per whorl observed on any branch becomes practically almost constant after the first 10 to 15 whorls. Even though there be a tendency to increase, the rate is so slow that in discrete variates such as we have here it would only be detected with very large numbers, while with ordinary numbers likely to be met in practice it would appear that there was a constant number of leaves. To show how slow the rate of change is we may determine at what position on primary branches the mean number of leaves would be 11, that is, one more than what we find as the highest mean number on the plants here dealt with. Put in another way, we may determine how many whorls would have to be successively formed in accordance with the law of growth which holds up to the 30th whorl before the *mean* number of leaves per whorl would become 11. To do this we have merely to substitute 11 for Y in our equation and solve for x. Doing this we have

$$\log (x - 0.8015) = \frac{3.04796}{1.3608} = 2.23977$$

whence

$$x = 177.5$$

or in round numbers, the mean number of leaves per whorl will not become 11 until the 177th or 178th whorl is reached! But the facts presented in the last section show that there is comparatively little divergence in the number of whorls to the branch (i.e., the length of the branch) in plants collected from different localities, provided they are taken at roughly the same period of the growing season. All show about the same number of whorls to the branch, and this number is very far short of anything like 100, even. There is no evidence whatever from our material that Ceratophyllum in a state of nature ever attains to such size as to have 175 whorls, or anything approaching that number, on primary branches. Our material includes several large plants, so that it can not be maintained that we are dealing with smaller-sized individuals than usually occur. In particular, plant 2 of Series IV was one of the largest Ceratophyllum plants I have ever seen. Yet, as

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has been seen in all our material, 30 whorls is the maximum for primary-branch length. We must conclude, then, I think, that under natural conditions the mean leaf-number per whorl becomes practically constant after the formation of from 15 to 20 whorls. This number is 10. To reach a mean leaf-number of 11 the branches must have more than 175 whorls, while to raise the mean to 12 would require the occurrence of primary branches with more than 900 whorls each! Such an occurrence is of course far out of the bounds of reasonable expectation.

TABLE 36.—*Observed and calculated mean leaf-number in successive whorls on primary branches. Series IV.*

Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.	Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.
1	7.441	7.304	+0.137	10	9.424	9.564	−0.140
2	8.453	8.359	+ .094	11	9.360	9.624	— .264
3	8.716	8.718	— .002	12	9.875	9.680	+ .195
4	8.988	8.939	+ .048	13	9.714	9.730	— .016
5	9.130	9.100	+ .030	14	9.750	9.777	— .027
6	9.211	9.226	— .015	15	9.900	9.820	+ .080
7	9.313	9.330	— .017				
8	9.491	9.419	+ .072				
9	9.550	9.495	+ .055				
				Sum of deviations			+ .230
				Average deviation per observation			+ .015

Another matter which demands consideration is this: We have reached our generalized law of growth from a study of plants collected at one place, namely, Carp Lake. Do plants from other localities follow the same law of growth? I think it is evident on general grounds that this is altogether likely to be the case, and table 34 and fig. 11 show very clearly that it is so. The law of the change in mean leaf-number with successive whorl formation must be the same to lead to such parallel results as we find on comparing any two series, as for example, Series I with Series IV or Series VI, etc. I propose to show in another way, however, that the law of growth which we have deduced is general for Ceratophyllum. A glance at fig. 11 indicates that the most marked difference between Series IV and Series I, II, or III in respect to the regression of leaf-number on position is that for corresponding positions the mean leaf-number is in general higher in Series IV than in the other three series. Now, suppose that without in the slightest changing the *shape* of our growth-curve, we simply change its *position* by moving it up on the y axis only 0.3 leaf. This will of course be done by simply increasing the value of the constant A by that amount. The result is shown in table 36 and graphically in fig. 12. The first column in the table and the zigzag line give the actually observed values for the mean

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leaf-number in the first 15 whorls on primary branches in Series IV, as given in table 36. The data are not carried farther than the 15th whorl, because from that point the material is too meager to yield very reliable means. This will be evident by examining table 30. The continuous curve is the graph of

$$Y = 8.2520 + 1.3608 \log (x - 0.8015)$$

the ordinates of which are given in the second column of the table. That is, it is our first growth curve, changed only by a uniform addition of 0.3 leaf in the absolute size of every whorl.

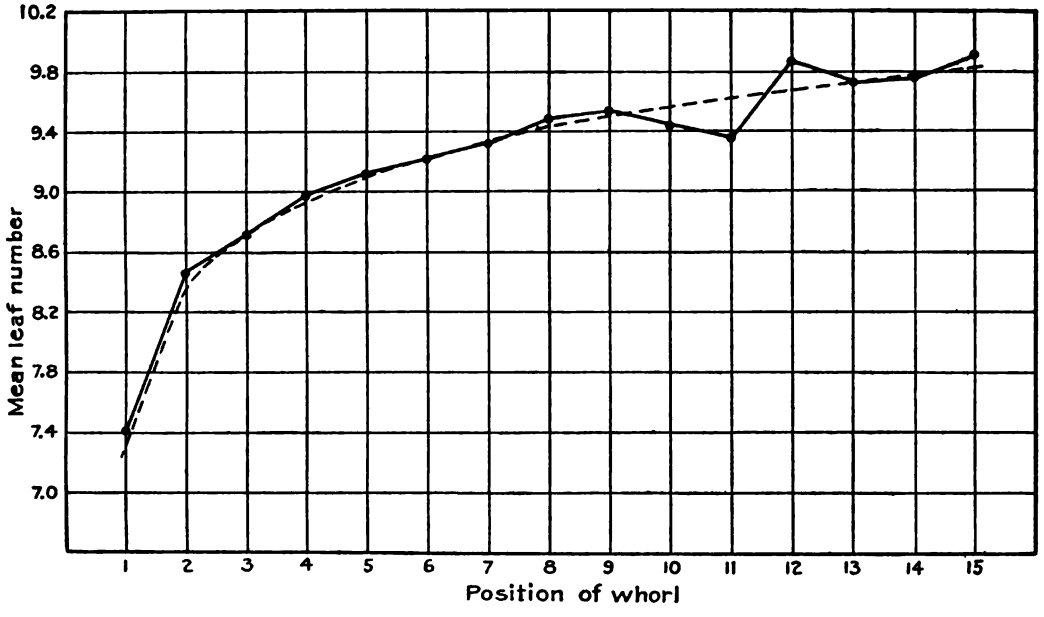

FIG. 12.—Regression of leaf-number on position and the fitted curve for Series IV. The ordinates give mean leaf-number and the abscissas position. ——— observation; - - - - - - theory.

It will be seen that the agreement between the actual observations and the values predicted by the growth curve is extraordinarily close. Of course there is some irregularity in the observations after the 10th whorl, but this is only to be expected when we remember that the means here are based upon comparatively few observations. Even at the worst the maximum deviation of observation from prediction is only a little over 0.2 leaf, while the average deviation is only 0.01 leaf.

This result seems to me to be of considerable importance, because, *in the determination of the shape of the growth curve the observations which we see it here expressing so very closely were in no wise taken into account.*

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TABLE 37.—*Correlation between leaf-number and position of secondary-branch whorls.*

SERIES I.

Number of leaves per whorl.	Position of whorl on branch.																	Total.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
6	17	2	2	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	22
7	20	4	1	1	...	1	...	...	...	...	...	...	...	...	...	...	...	...	27
8	10	15	7	2	5	1	1	1	...	1	...	...	...	...	...	...	...	...	43
9	...	7	11	11	5	3	1	2	1	...	...	1	...	...	...	...	...	...	42
10	...	...	1	1	1	1	1	...	1	1	1	...	1	...	...	...	...	...	9
Total	47	28	22	16	11	6	3	3	2	2	1	1	1	...	...	...	...	...	143

SERIES II.

5	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2
6	30	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	32
7	18	12	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	33
8	8	24	14	5	3	1	...	1	...	...	...	...	...	...	...	...	...	...	56
9	2	13	17	19	12	8	6	2	...	...	...	...	...	...	...	...	...	...	79
10	...	1	6	3	4	4	3	2	2	...	1	1	1	...	...	...	...	...	28
11	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
Total	61	52	40	27	19	13	9	5	2	1	1	1	1	...	...	...	...	...	231

SERIES III.

6	24	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	24
7	8	8	1	1	1	...	...	...	...	...	...	...	...	...	...	...	...	...	19
8	8	15	3	4	...	1	1	...	2	...	...	...	...	...	...	...	...	...	34
9	...	6	13	11	10	7	6	4	1	2	...	...	...	...	...	...	...	...	60
10	...	...	4	3	3	3	3	4	4	2	1	1	...	...	...	...	...	...	28
Total	40	29	21	19	14	11	10	8	7	4	1	1	...	...	...	...	...	...	165

SERIES IV.

6	7	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	9
7	61	21	4	7	3	1	1	...	...	...	...	...	...	...	...	...	...	...	98
8	34	43	37	20	18	8	4	6	2	2	2	...	1	...	...	...	...	1	178
9	5	31	33	41	28	20	20	10	11	2	...	1	1	1	...	1	...	...	205
10	...	1	8	5	8	10	10	10	10	14	12	11	9	7	5	3	2	...	125
11	...	...	...	...	...	1	...	...	...	...	1	...	...	...	...	...	...	...	2
Total	107	98	82	73	57	40	35	26	23	18	15	12	11	8	5	4	2	1	617

SERIES I, II, AND III COMBINED.

5	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2
6	71	4	2	1	...	...	..	...	...	...	...	...	...	...	...	...	...	...	78
7	46	24	5	2	1	1	...	...	...	...	...	...	...	...	...	...	...	...	79
8	26	54	24	11	8	3	2	2	2	1	...	...	...	...	...	...	...	...	133
9	2	26	41	41	27	18	13	8	2	2	...	1	...	...	...	...	...	...	181
10	...	1	11	7	8	8	7	6	7	3	3	2	2	...	...	...	...	...	65
11	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1
Total	147	109	83	62	44	30	22	16	11	7	3	3	2	...	...	...	...	...	539

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That is to say, we find that a mathematical function deduced solely from data given by Ceratophyllum plants collected at Carp Lake expresses perfectly the method of growth of Ceratophyllum plants collected at Ann Arbor. This seems to me to amount to a demonstration that our growth curve is an expression of a real and fundamental morphogenetic law in Ceratophyllum and not a mere chance result, or due to any skillful figure juggling.

By changing the position of the curve slightly in the opposite direction we obtain a very fair graduation of the regression in Series V, though on account of the fact that Series V and VI include spring plants in which we have the results of a part of two seasons' growth, as has been pointed out above (p. 15), the fit in these cases is not so good as in the other series.

The result shown in fig. 12 enables us to reach a further interesting conclusion. We see, namely, that in our fundamental growth equation

$$Y = A + C \log (x - a)$$

it is the constant A which is affected by environmental differences. That is, *the absolute size of the elements of the developing system given by a Ceratophyllum branch is modified by environmental differences, but the law which describes the proportionate differentiation of the elements is independent of the environmental history of the plant.* Thus we are able by statistical analysis to separate clearly and definitely the effects of external environmental factors and internal form-determining factors in this case. The constant A takes different values in populations living in different environments, while the portion $C \log (x - a)$ remains unaltered, or is only very slightly altered, and we may therefore look upon A as the "environmental constant."

TABLE 38.—*Correlation between leaf-number and position of secondary-branch whorls.*

Series.	r.	η.	Table.
I	0.601±0.036	0.712±0.028[a]	37
II	.688± .023	.801± .016	37
III	.692± .027	.816± .018	37
IV	.650± .016	.727± .013	37
I, II, and III combined	.671± .016	.784± .011	37

[a] As before, the probable error of the correlation ratio η is calculated from the short formula.

So far we have been dealing with primary-branch whorls in the discussion of the regression of leaf-number on position. It remains to determine in how far the same relations which we have found for primary branches hold for other divisions of the plant. We may turn first to the consideration of whorls on secondary branches.

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The correlation tables showing the relation between number of leaves in the whorl and position on the branch for this division of the plant are given in table 37.

The correlation coefficients (r) and correlation ratios (η) deduced from the preceding table are given in table 38. From this table the following points are to be noted:

(a) As in the case of the primary branches there is a high correlation between the number of leaves in the whorl and position on the branch. Comparing the values of the correlation constants for secondary branches with those for primary branches given in table 33 above, we see that

TABLE 39.—*Mean number of leaves in successive whorls on secondary branches.*

Position of whorl.	Mean number of leaves.				
	Series I.	Series II.	Series III.	Series IV.	Series I, II, and III combined.
1	6.851	6.633	6.600	7.346	6.694
2	7.964	7.981	7.931	8.082	7.963
3	8.364	8.650	8.842	8.549	8.651
4	8.625	8.926	8.071	8.603	8.823
5	8.636	9.053	9.182	8.719	8.954
6	8.667	9.231	9.200	9.050	9.100
7	9.000	9.333	9.200	9.114	9.227
8	8.667	9.200	9.500	9.154	9.250
9	9.500	10.000	9.286	9.348	9.455
10	9.000	11.000	9.500	9.667	9.571
11	10.000	10.000	10.000	9.800	10.000
12	9.000	10.000	10.000	9.917	9.667
13	10.000	10.000	.....	9.727	10.000
14	.....	.....	.....	9.875	.....
15	.....	.....	.....	10.000	.....
16	.....	.....	.....	9.750	.....
17	.....	.....	.....	10.000	.....
18	.....	.....	.....	8.000	.....

they are without exception higher in the case of the secondaries. The reason for this is found in part in the fact that the secondaries are shorter than the primary branches. Consequently they do not have at the distal ends of the long branches the long string of whorls with, as has been shown above (p. 62), a very nearly constant number of leaves. These distal whorls, from about 15 on, operate in the case of the primaries to lower the correlations. To get a fair test of the relative degree of the positional correlations in the two orders of branches we must compare branches of roughly the same length. From table 37 we see that the secondary branches of Series I, II, and III run up to 13 whorls, while in Series IV they go to 18 whorls. If, now, we calculate the coefficient of correlation between leaf-number and position, for the first 13

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whorls on primary branches in Series I, II, and III combined, we find a value

$$r = 0.555.$$

In the case of Series IV, since the primary branches (cf. table 30) only extend to 24 whorls, and the total frequency beyond the 18th whorl is only 13, it is obvious that for all practical purposes the constants given in table 33 for the primary-branch correlation are directly comparable with those for the secondaries given in table 38. Comparing the primary-branch values with the corresponding ones for secondary branches in table 38 it is clear that apart from the reduction of the correlation caused by the great length of primary branches there is still a higher correlation between leaf-number and ordinal position of the whorl in secondary branches than in primaries. The significance of

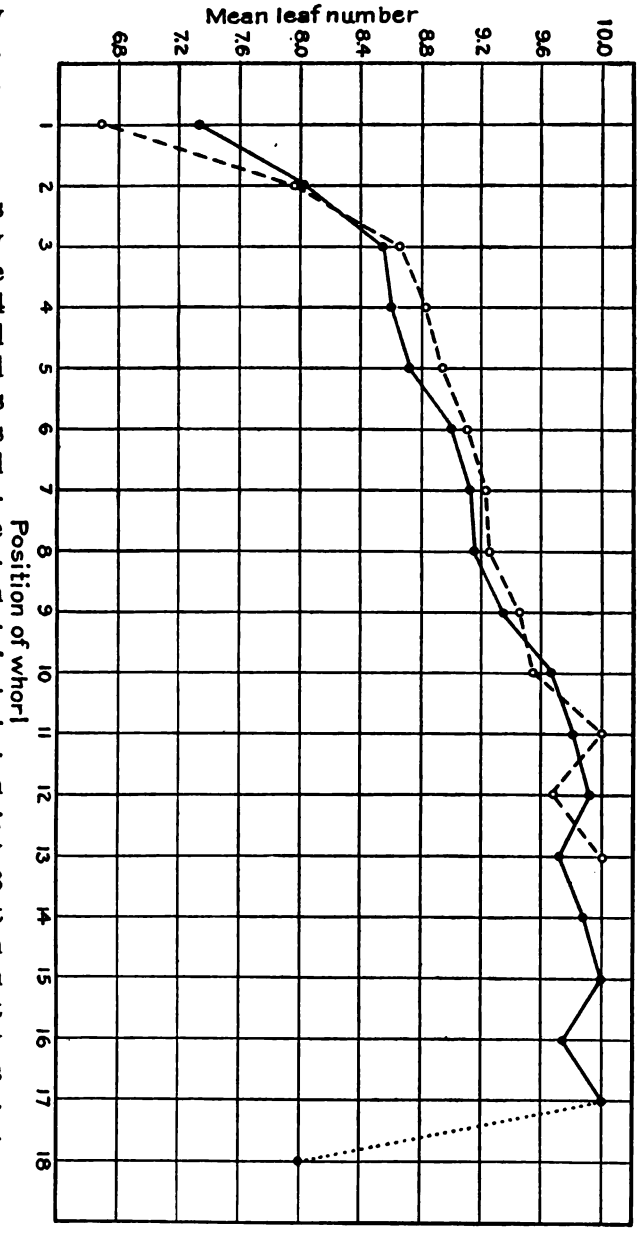

FIG. 13.—Regression of leaf-number on position in secondary-branch whorls. Series I, II, and III combined, o- - - - - - ; Series IV, ●———— .

this fact will be pointed out later, when certain other results are in hand.

(*b*) There is the same uniformity in the correlations for the different series as was observed in the case of the primary branches.

(*c*) It is obvious from the values of r and η that the regressions are not linear.

The precise character of the regression of the leaf-number on position is given in table 39. In this we have for each of the first four series and the combined Series I, II, and III, the mean number of leaves for each position on the branch.

It is at once apparent that the secondaries start with a smaller mean number of leaves to the whorl than do primaries, but that the increase in the first few whorls from the origin is more rapid than in primary branches. Unfortunately in the case of secondary branches the number of observations on which the means are based gets small very quickly, so that the results begin to be irregular even before we reach the 10th whorl. The figures in the table show these points, but they are brought out more clearly in the diagrams in fig. 13, which show graphically the regression lines for Series I, II, III, and IV.

TABLE 40.—*Comparison of observed and calculated mean leaf-number for successive whorls of secondary branches. Series I, II, and III combined.*

Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.	Position of whorl.	Observed mean leaf-number.	Calculated mean leaf-number.	Difference.
1.....	6.694	6.630	+0.064	9.....	9.455	9.513	—0.058
2.....	7.963	8.013	— .050	10.....	9.571	9.604	— .033
3.....	8.641	8.485	+ .166	11.....	10.000	9.685	+ .315
4.....	8.823	8.778	+ .045	12.....	9.667	9.758	— .091
5.....	8.954	8.991	— .037	13.....	10.000	9.825	+ .175
6.....	9.100	9.158	— .058				
7.....	9.227	9.295	— .068	Sum of deviations.....			+ .208
8.....	9.250	9.412	— .162	Average deviation per observation.....			+ .016

From these diagrams we see that the general features of the regression are essentially the same in secondary as in primary branches. There is clearly a functional relation of very much the same sort between the number of leaves to the whorl and the order of formation of the whorl. To determine the nature of this functional relation, we may in the light of our experience with primary branches assume at once that it is of the form

$$y = A + C \log (x - a)$$

and proceed to fit a curve of this type to the data by the method followed in the former case. This was done, using as material the combined

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Series I, II, and III, as before. In this case, however, the origin of y was taken at 6.6 instead of at 7, as in the other case. The reason why this was done will be obvious to the mathematical reader.

The curve obtained was

$$y = 1.2662 + 1.8024 \log (x - 0.7939)$$

whence, taking the origin of y at 0 we have finally

$$Y = 7.8662 + 1.8024 \log (x - 0.7939) \quad . \quad . \quad . \quad . \quad . \quad \text{II}$$

where Y indicates mean number of leaves to the whorl and x indicates ordinal position on the branch. The observed and calculated ordinates are given in table 40. The actual observations and the fitted curve are shown in fig. 14. Considering the paucity of observations at the upper end of the range, a better graduation could not reasonably be expected. We conclude, then, that the same type of curve expresses the regression in secondary branches as in primaries. Or, in other words, *the differentiation of successively formed whorls follows the same general law in both primary and secondary branches.*

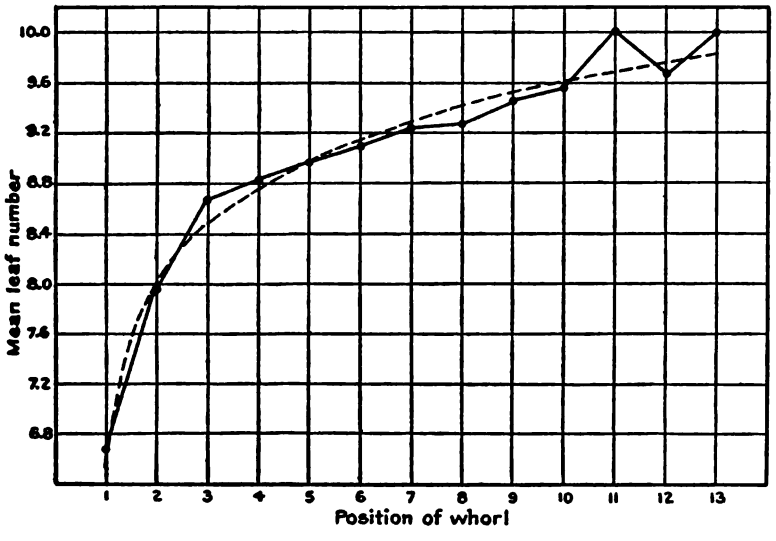

FIG. 14.—Regression of leaf-number on position in secondary branches. Series I, II, and III combined. Observations, ●———●; fitted curve, ·····.

Having seen that the growth curve is fundamentally the same for the two orders of branches, we may next examine the differences in the two cases, and see what they signify. We may first notice how the increment in mean leaf-number per unit advance in position compares in the case of secondaries with what it is in primaries, for corresponding

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whorls in the two cases. The value of the constant C in the case of the secondaries ($=1.8024$) shows us at once that the increment in Y per unit change in x will be greater in the secondary-branch whorls than in the primary. That this in fact is the case is obvious enough to the eye if we compare fig. 14, with plate I. The upward slope of the secondary curve is much more rapid than is that of the primary curve. The fact may be shown in another way. The successive increments in mean leaf-number for the first 10 whorls of primary and secondary branches are given in table 41.

TABLE 41.—*Increment in leaf-number in successive whorls.*

Increment in mean leaf-number between—	On primary branches.	On secondary branches.
First and second whorls	1.055	1.383
Second and third whorls	.359	.472
Third and fourth whorls	.221	.293
Fourth and fifth whorls	.161	.213
Fifth and sixth whorls	.126	.167
Sixth and seventh whorls	.104	.137
Seventh and eighth whorls	.089	.117
Eighth and ninth whorls	.076	.101
Ninth and tenth whorls	.069	.091

It is evident that the increments are larger on the secondary branches. The nature of the change in the increment is very clearly shown if we plot the data from table 41 to the same scale for the two orders of branches. This has been done with the result shown in fig. 15.

We see that though the secondary branches start lower, they attain any designated mean leaf-number in a smaller number of whorls. Thus while in the case of the primary branches a *mean* leaf-number per whorl of 11 would only be reached after the formation of 175 successive whorls, the secondaries would reach this mean after the formation of only 56 whorls in round numbers (55.58 exactly). That is to say, if we may speak in terms of analogy, the morphogenetic mechanism attains its results more rapidly in the case of the secondary branches. This is an expression of the fact noted above (p. 77) that the positional correlation is higher in secondary than in primary branches. The law of growth in the plant is, as we have seen, that the mean leaf-number per whorl increases with successive whorl formation, the rate of increase at any point varying inversely as the number of whorls which have been formed up to that point. Clearly the production of a maximum mean leaf-number may be regarded as the "end" towards which the morphogenetic process here tends. But the secondaries attain this "end" more quickly than do the primaries; that is, with the formation of fewer successive whorls. If, merely as an analogy, we

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may compare the developing branches of a Ceratophyllum plant with a machine, of which the whorls are the product, we may say that the machine works more smoothly the longer it runs.

The fact that the increments in mean leaf-number with successive whorl formation are greater in the case of secondary branches is shown in the growth equation by the higher value of the constant *C*. This indicates that *C* may be regarded as the constant which expresses the action of the internal formative factors, in contradistinction to *A*, which, as we have seen above (p. 75) in the case of primary branches, expresses the effect of external environmental conditions. We should expect *C*, then, to remain practically constant for the same division of the plant

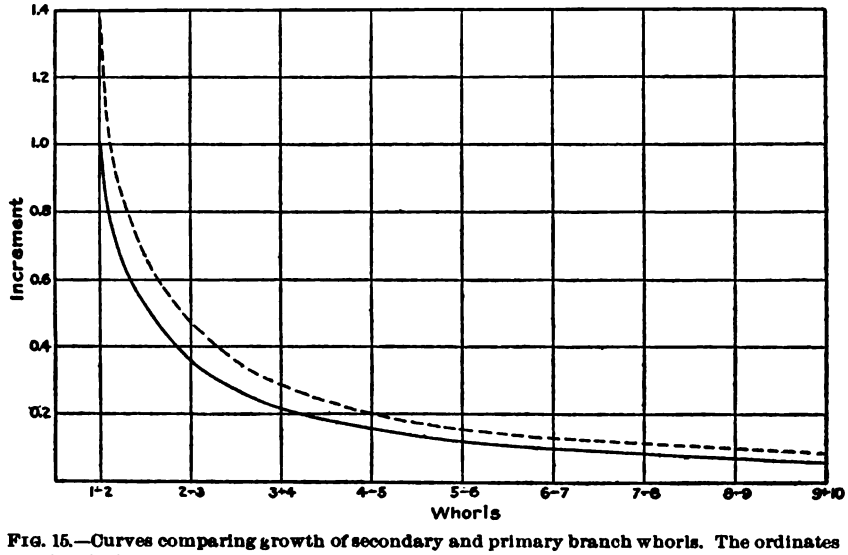

FIG. 15.—Curves comparing growth of secondary and primary branch whorls. The ordinates give the increments in mean leaf-number as we pass to successive whorls, the positions being given by the abscissas. Primary-branch whorls ———; secondary-branch whorls .....

(i.e., primary or secondary branches) without regard to external influences, while *A* changes with change of environmental conditions. In other words, it would appear that external conditions affect chiefly the absolute size of the elements of the plant while the internal morphogenetic factors which determine the way in which the proportionate differentiation of the elements shall occur are practically independent of environmental change. These relations hold for primary branches very clearly, so far as the present material goes. We might test the matter for the secondaries in the same manner as before by determining whether with an appropriate change of the constant *A* in the secondary-branch growth equation (II) which has been deduced from Carp Lake

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data solely, we could get a reasonable graduation of Ann Arbor material. Unfortunately the Series IV data for secondaries are so meager that the results are rather irregular. The number of plants is not large enough to get rid of the disturbing influence of the individuality of a single large specimen. This especially shows itself in the first whorls of secondary branches in this series, where we get an abnormally high mean, due to the marked tendency for one of the plants in this series to have exactly 7 leaves in these whorls. If, however, we change the position of the growth-curve (equation II) by lowering it 0.1 of a leaf on the y axis, it represents the data for Series IV, with the exception of the first whorl, with very considerable accuracy. Thus, taking the first 10 whorls (after this the observations are too few to give reliable means), I find the total deviation between observation and theory to be $+0.253$, giving an average deviation per observation of 0.025. This is a sufficiently close agreement to justify the contentions made that (*a*) environmental differences affect chiefly the absolute size of the elements, and (*b*) that the essential character of the differentiation with growth is practically independent of environmental influences. We could of course get a better graduation of the Series IV material by specially determining all the constants of the curve anew from that data, but what I have tried to show is that we get for all practical purposes a sufficiently good fit by simply shifting slightly the position of the curve deduced from the other series, this alteration being merely to take into account the difference in absolute size between the two sets of plants.

Summing up, then, we see *that the same law of differentiation of whorls with growth holds for secondary as for primary branches.* The chief difference in the two cases is that the change in successively formed whorls is, at any given point, greater in secondary than in primary branches.

We have now to consider the question of whether the same law which we have found for secondary and primary branches holds for the other divisions of the plant (main stem and tertiary branches). We may take up first the main stem. It is of course to be expected that the relations are not essentially different here. Unfortunately it is impossible to test the matter directly in the way which has been used for the other divisions, because of lack of material. A plant may have 50 or more primary branches, but of course it has only one main stem. Therefore, to get satisfactory means for main-stem whorls in particular positions it would be necessary to have a very considerable number of plants. There is a further difficulty in the case of the main stem. Ordinarily the plants have several inches of the lower (proximal) end of the main stem embedded in the soft débris and mud of the bottom.

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In almost every case one finds that the whorls which were originally present in this region of the plant have been in whole or in part destroyed, so that it becomes quite impossible to tell how many leaves they bore. Only scars and short stumps of leaves remain to indicate the original presence of whorls. It is probable that the destruction of the leaves in this region is due in the main to the action of plant-feeding aquatic animals. In any event it is impossible to get a determination of the regression of leaf-number on position in the first-formed whorls of the main stem. The extent to which this destruction of leaves has gone varies very much in different plants. In some cases only a few whorls are found to be mutilated, while in other plants a considerable number are completely destroyed.

TABLE 42.—*Correlation between leaf-number and position in main-stem whorls. Series I, II, and III combined.*

Leaves per whorl.	Position of whorl.									
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	Total.
6.....	2	2	...	1	...	...	...	...	...	5
7.....	1	3	3	1	1	...	...	...	...	9
8.....	5	5	7	3	3	2	1	...	...	26
9.....	21	24	18	16	15	10	2	2	...	108
10.....	15	22	30	47	35	17	17	8	4	195
11.....	...	3	10	6	6	4	...	...	...	29
12.....	...	1	1	...	...	...	...	...	...	2
Total...	44	60	69	74	60	33	20	10	4	374

$r = 0.238 \pm 0.033$.

In order to show the nature of our material, so far as it goes, in this respect, table 42 has been prepared. This gives for Series I, II, and III combined the actually observed frequencies of main-stem whorls with various leaf-numbers, in different positions. Position is indicated in the same way here as in the case of the branches; that is, the most proximal whorl on the stem is numbered 1, the whorl next it 2, and so on in regular succession. In the cases where the main stem has dichotomized the whorls on each subdivision are numbered in order, both beginning at the same point. For example, if the main stem divided after the formation of the 25th whorl, the first whorl on *each* of the subdivisions would be numbered 26, since both occupy the same position relative to the main axis. Since the whole number of entries for main-stem whorls is so small, I have not entered each whorl separately in the table here shown, but have combined them in groups of 10. This, of course, would not be legitimate if we expected to get very fine results, but the material is too scanty to give close results in any event, and by arranging it in this way we are able to see better the general trend.

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It is seen at once by mere inspection of the table that there is clearly a change in the mean number of leaves per whorl, with successive whorl formation. The precise amount of this change is shown in table 43, which gives the actual mean for each array of table 42.

TABLE 43.—*Regression of leaf-number on position in main-stem whorls.*

Position of whorl.	Mean number of leaves per whorl.	Position of whorl.	Mean number of leaves per whorl.	Position of whorl.	Mean number of leaves per whorl.
1–10	9.045	31–40	9.689	61–70	9.800
11–20	9.233	41–50	9.700	71–80	9.800
21–30	9.580	51–60	9.697	81–90	10.000

This result shows that *in main-stem whorls, just as in primary and secondary branch whorls, there is a definite relation between the number of leaves and the position on the axis. The later-formed whorls tend to have a higher mean number of leaves than those formed earlier.* The data of table 43 are shown graphically in fig. 16.

The increase in mean leaf-number in main-stem whorls is clearly very gradual. We have now to determine whether it is according to the same law which holds for other divisions of the plant. On account of the paucity of material we can not get at this directly as we have in the other cases, but must resort to an indirect method. For reasons which have been stated above, we know nothing about how the main-stem curve starts. The first array in table 42 (whorls 1 to 10) is unfortunately largely composed of whorls above the fifth, the lower ones being in most cases broken. The consequence is that the mean for this group has an unduly high value. Further, there can be no doubt that the main-stem curve actually starts at a considerably higher level than does that for primary branches, so that it would be obviously unfair to compare the absolute values predicted from our primary-branch growth curve (equation I) with main-stem means. The fairest way of approaching the problem seems to me to compare the *increment* in mean leaf-number occurring between whorls in different situations on the main stem with the *increment* between similarly situated whorls on primary branches as predicted by equation I. If there is reasonable agreement between the observed and predicted increments we may fairly say that the growth and differentiation of leaf-whorls follows the same law in the main stem and the branches. The data for this comparison are given in table 44.

On the whole these results are quite satisfactory. Of course there is wide divergence between observed and predicted results at the two ends of the series. At the lower end (whorls 5 to 15) the observed increment is much too small, but, as has been pointed out, our first mean

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gives no adequate idea of the actual condition at the proximal end of the main stem. It is altogether too high, because of the destruction of the earlier whorls in most cases. At the upper end (75 to 85 whorls) we have only four whorls to base the mean on — an obviously insufficient number. Leaving out of account the upper and lower ends of the series, we have quite as good agreement between observation and theory as could be expected. Or, we conclude that *the same law of growth describes the change in mean leaf-number in successively formed whorls, whether the whorls are borne on the main stem or on primary or secondary lateral branches.*

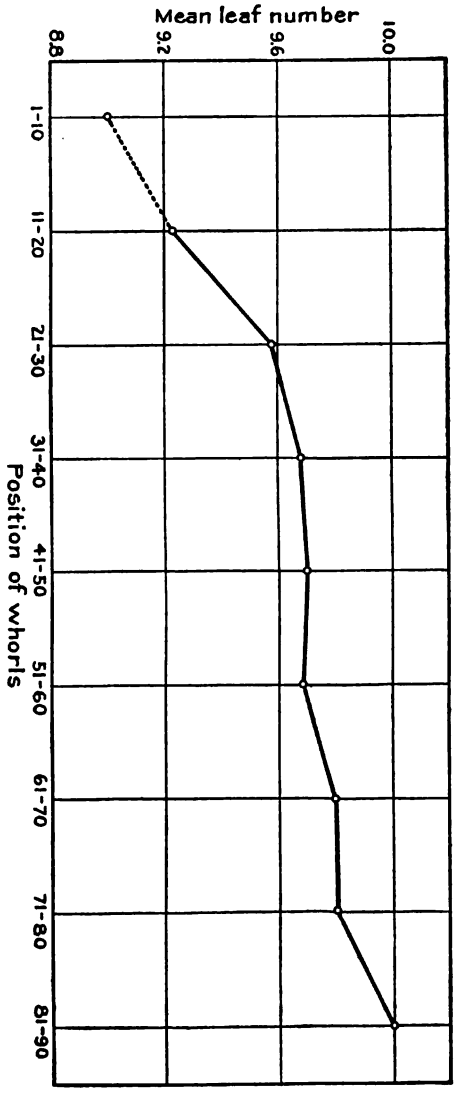

FIG. 16—Regression of leaf-number on position in main-stem whorls, Series I, II, and III combined.

The discussion of main-stem whorls has been based on the data of Series I, II, and III. The other series lead to exactly the same result, and consequently it does not seem necessary to consider them in detail in this connection.

We come finally to the consideration of tertiary-branch whorls from the standpoint of positional differentiation. The same difficulty is met here as in the case of the main stem, namely, very meager material. We have, however, sufficient data to get an idea of the general conditions among the whorls in this division of the plant. Taking as before the combined Series I, II, and III, we have the observations set forth in table 45. From this table I find

$$r = 0.603 \pm 0.059$$
$$\eta = 0.878 \pm 0.021$$

We conclude, then, that just as in other divisions of the plant there is a considerable degree of correlation between leaf-number and order

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of formation of tertiary-branch whorls. We further note that the correlation between these two characters is distinctly higher in tertiary-branch whorls than in main-stem or primary-branch whorls. The correlation coefficient is of about the same order of magnitude for tertiaries as for secondaries, but the correlation ratio (which is the better measure in these cases of skew correlation) is markedly higher for the tertiaries than for secondaries (cf. table 38, *supra*).

TABLE 44.—*Comparison of increments in mean leaf-number occurring between every ten whorls on (a) the main stem, and (b) primary branches. Series I, II, and III combined.*

Increment in mean leaf-number between—	Observed on main stem.	Predicted from primary branches (equation I).	Difference.
5th and 15th whorl	0.188	0.720	.....
15th and 25th whorl	.347	.315	+0.032
25th and 35th whorl	.109	.203	— .094
35th and 45th whorl	.011	.153	— .042
45th and 55th whorl	— .003	.121	— .124
55th and 65th whorl	.103	.100	+ .003
65th and 75th whorl	.000	.085	— .085
75th and 85th whorl	.200	.....	.....

The change in mean leaf-number with advance in position is shown in table 46, giving the means of the arrays of table 45. From this table the following points are to be especially noted:

(*a*) The tertiary branches start at the first whorl with a lower mean number of leaves than do either primaries or secondaries.

TABLE 45.—*Correlation between leaf-number and position in whorls on tertiary branches. Series I, II, and III combined.*

Leaves per whorl.	Position of whorl.						
	1	2	3	4	5	6	Total.
6	12	...	...	...	...	...	12
7	8	3	1	...	...	...	12
8	2	8	...	...	...	...	10
9	...	4	4	4	1	...	13
10	...	...	2	1	3	2	8
Total	22	15	7	5	4	2	55

(*b*) The rate of increase in mean leaf-number with successive whorl formation, so far as we can judge from our present material, is much more rapid in the case of the tertiaries than in the other branches. That is, if we regard the production of a high mean leaf-number as the "end" towards which the growth processes are tending, this "end" is

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apparently attained with the production of fewer whorls in the case of tertiaries than in either of the lower-order branches.

TABLE 46.—*Regression of leaf-number on position in tertiary-branch whorls.*

Position of whorl.	Mean number of leaves.	Position of whorl.	Mean number of leaves.
1	6.545	4	9.200
2	8.067	5	9.750
3	9.000	6	10.000

We have now to consider the question as to whether the differentiation of successive whorls which exists here is in accord with the same general type of growth curve which has been demonstrated for the other branches. We can of course say *a priori* that it is altogether likely that this is the case, but it is desirable to see just what result we get from the actual data, even though they are small in point of numbers. The data are too few to make it worth while to attempt to fit a special curve for them, nor is it necessary to do this to bring out the point. What we wish to find is whether in the case of the tertiaries the *rate* of increase in mean leaf-number diminishes as the number of whorls formed increases. It is clear that one simple test of this would be to determine whether the ratio between the increments in leaf-number in successively formed whorls diminishes. If it does, then clearly the rate of increase is diminishing. Taking the first four whorls, we have the following absolute increments in mean leaf-number:

Between first and second whorls 1.522
Between second and third whorls ..... .933
Between third and fourth whorls ..... .200

These yield the following ratios:

$$\frac{0.933}{1.522} = 0.613$$

$$\frac{0.200}{0.933} = 0.214$$

Or we conclude that, so far as we can form any judgment from the present data, *the rate of increase in mean leaf-number in tertiary-branch whorls decreases as the number of successively formed whorls increases. Or, in other words, it appears that the differentiation of the whorls on the tertiary branches follows the same law which has been shown to hold for the other axial divisions of the plant.*

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SUMMARY OF SECTION.

We may now put together in orderly form the chief results which have been gained in this section of the paper. It has been shown that:

(*a*) There is a positive correlation between the number of leaves to the whorl and position of the whorl on the plant, or, since in a plant growing in the manner in which Ceratophyllum does, position on the plant is determined by the order of the formation of the organ or character under consideration, there is a correlation between the number of leaves to the whorl and the ordinal rank in the process of successive whorl formation.

(*b*) This correlation is considerable in amount. It is lowest for the main-stem whorls, and increases steadily in the higher axial divisions of the plant (primary, secondary, and tertiary branches).

(*c*) The regression of leaf-number on position is not linear, but logarithmic.

(*d*) The mean number of leaves to the whorl *increases* with successive whorl formation according to the equation

$$y = A + C \log (x - a)$$

where y denotes the mean number of leaves per whorl, x the position of a whorl on an axial division of the plant, and A, C, and a are constants. Stated in words, the law of differentiation with growth in Ceratophyllum is: *The mean number of leaves per whorl increases with each successive whorl, and in such a way that not only does the absolute increment in each leaf-number diminish, but also the rate of increase diminishes as the ordinal number of the whorl, measured from a fixed point, increases.* This may be, for convenience, designated as the *first law of growth* in Ceratophyllum. It means, broadly speaking, that the form of any particular whorl of a Ceratophyllum plant is a function (in the mathematical sense) of the number of whorls which have been produced before it on the same axis.

(*e*) The same law of growth holds (with appropriate changes of the constants) for all axial divisions of the plant (main stem, primary, secondary, and tertiary branches).

(*f*) The absolute size of the elements of the developing system given by an axial division of a Ceratophyllum plant is modified by environmental differences, but the proportional differentiation of the elements is in accord with the same law in plants from different environments.

(*g*) The *absolute increment* in mean leaf-number between similarly situated successive whorls is least on the main-stem, and increases regularly in each of the higher axial divisions (primary, secondary, and

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tertiary branches). That is to say, a given mean number of leaves per whorl is produced with the formation of the *least* number of consecutive whorls in the case of tertiary branches; more whorls are required to attain the same result on secondaries, more still on primaries, and most of all on the main stem.

Before going on to other subjects I wish to discuss certain points brought out by the results of this section which could not well be taken up till all the results for positional leaf differentiation were in hand. In the first place, we note that from the correlation tables for the characters, position, and leaf-number given in this section (tables 30–32, 37, 42, and 45) it is a simple matter to build up piece by piece the gross frequency distributions for all whorls on the plant, such as are given in an earlier section of the paper (e. g., table 1). In other words, the arrays of the correlation tables form, so to speak, the dissected elements of our earlier gross frequency distributions. It has been possible in the present case to carry out this process of dissection of variation curves with considerably greater completeness than has hitherto usually been the case. The results of this procedure will, I believe, repay careful study from several different points of view.

In order to bring out more clearly the general features of the analysis of the frequency distributions, I have resorted to the graphical method, with the result shown in plate II.

In plate II the whorls belonging to different divisions of the plant are represented in different colors, main-stem whorls being given by blue, primary-branch whorls by red, secondary-branch whorls by green, and tertiary-branch whorls by yellow. The data are for Series I, II, and III combined. The abscissas give number of leaves per whorl and the ordinates, frequencies. Instead, however, of representing merely the total height of the ordinates, the frequency of each size of leaf is proportionately divided to show where whorls are located on the plant as a whole and also on the individual axes. These proportional divisions are indicated by the horizontal lines, and the areas they include represent the frequency of whorls in the positions indicated by the Arabic numerals. In order to avoid too great complexity in the diagram the whorls have been to some extent grouped. In the case of the main stem each 10 succeeding whorls were grouped together; in the primary branches the 1st to the 10th whorls, inclusive, are given by single whorls, and from that point to the end of the branch in groups of 5; in the secondary branches the first 6 whorls are given singly, while the remainder of the whorls (7th to 13th inclusive) are in a single group; the first two tertiary-branch whorls are given singly, and the remainder (3d to 6th, inclusive) together. The smooth curves are the graphs of the equations given on pages 23 and 24.

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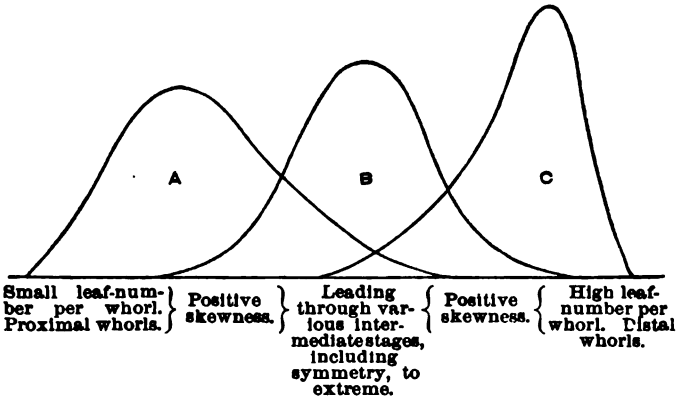
The diagram brings out very sharply a number of points. In the first place we see that, whatever the part of the plant, first whorls contribute proportionately very largely towards the frequencies on the low leaf-numbers. As we go out towards the distal end of the branch or the main stem the proportionate frequency of 9 and 10 leaved whorls increases. Thus if we compare the rectangle representing 7-leaved whorls with that for 10-leaved whorls we see at once that the subdivisions of the first *decrease* for each division of the plant as we go towards the top of the diagram, while the subdivisions of the latter *increase*. This means of course that the skewness of the distributions is changing in the manner schematically indicated in the following diagram:



A and *C* would represent the extreme conditions of proximal and distal whorls, while *B* would represent one of a whole series of intermediate stages passed through as we go from *A* to *C*. It will be understood that this diagram is purely schematic, but fairly represents the essential facts very closely. The same stages as those indicated may indeed be seen in plate II, or in the correlation tables (cf. *supra*) on which it is based, while a careful examination of the data will leave no doubt in the mind of the reader that the general trend of the frequency distributions in respect to skewness is fundamentally that indicated. We see, then, that homologous organs on the same individual plant run through the whole gamut of skewness from positive (*A*), through perfect symmetry* to negative (*C*). The phenomenon of skew variation stands forth in this case, free of doubtful interpretation through selection or any similar factor, clearly and definitely as a phenomenon of growth. In

*Cf. for example the distribution for the third whorl on primary branches in Series I, II, and III combined.

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the face of facts of this kind it is difficult to understand how anyone can be so firmly convinced of the *Allgemeingültigkeit* of the normal or Gaussian law, as some biologists still are [cf. for example, Ranke and Greiner (:04)]. Skewness in variation is a very real biological phenomenon, which may be changed and modified, not only in degree, but in direction, by various biological factors like growth, as, for example, in the present case, or environmental influences,* etc.

The general features of our first law of growth are very well brought out graphically by the diagram of plate II. Thus we see clearly that for all divisions of the plant the *proportionate* frequency of whorls with high leaf-numbers becomes greater the longer the plant grows, though at a decreasing rate. This of course results in the increase in mean leaf-number which has been discussed in this section of the paper.

It is also of some interest to see graphically the proportion of whorls which the different axial regions contribute to the plant as a whole. Primary branches manifestly outweigh any other part of the plant.

With a knowledge of the law of positional differentiation of whorls we are able to interpret many of the facts regarding variation in Ceratophyllum which were before obscure. These interpretations will be so obvious to anyone who has followed the results so far set forth that it is not worth while to go over all of them in detail. A few cases only need be cited as illustrations. Thus, on page 18 it was seen, when the gross frequency distributions for Series I, II, and III were compared, that "Series I has the lowest frequency of whorls with 10 leaves, Series II has about 3 per cent more 10-leaved whorls, while Series III has 4 per cent more of such whorls than does Series I." The explanation of this progressive difference is now clear. A reference to page 13 will recall the fact that the dates of collection for Series I, II, and III were respectively July 22, August 18, and August 25. The proportionate frequency of 10-leaved whorls varies directly as the date of collection, which is exactly what would be expected from our law of growth, since as growth goes on there is an ever-increasing tendency towards the addition of whorls with 10 or a higher number of leaves.

It has appeared at various points throughout the paper that the gross frequency distributions for Series V and VI were different in their characteristics, both from all the other series considered and from each other. Yet, as has been seen in this section and will be more fully brought out later, these Series V and VI plants follow the same laws of growth differentiation as do the others. The explanation of their apparent abnormality is to be found principally in the fact that in the

*E. g., see Pearl (:06).

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main they were plants which had wintered over without breaking up (cf. p. 15, *supra*). When this happens and vigorous growth begins again in the spring, we should expect to find the plants bearing branches* of high average length and having an unusually large proportion of all their whorls borne on primary branches. Reference to tables 25 and 26 shows exactly this to have been the case in Series VI. But on long branches according to our law of growth there will be a great preponderance of 10-leaved whorls. Hence we see the reason for the result previously obtained, viz, "The polygon for Series VI is not quite smooth and regular, yet differs from all the others in having as the most frequent class 10-leaved whorls." Series V differed from all the other series in its gross frequency distributions in showing an unusually high proportionate number of 7-leaved whorls. This arises from the fact that the two large plants in this series (1 and 7), when the spring growth began, threw out an unusually large number of new lateral branches (secondaries, tertiaries, and quaternaries). At the time the collections were made these branches had not attained any considerable length. Hence we have a preponderance of *short* branches in this series, and, as indicated by the law of growth, we should in consequence expect a considerable increase in the relative frequency of whorls with low leaf-number, which is just what we find.

It hardly requires discussion to make it evident that the facts embodied in our law of growth explain how the characteristic values and differences in the variation constants for different regions of the plant, as set forth in an earlier section, arise. It was found that the older the portion of the plant the higher was the mean number of whorls. But the reason for this is now clear, since the older portions will have grown longer than the younger and produced more whorls with high leaf-numbers. It will be seen later that the differences in variation in different portions of the plant are to be accounted for similarly.

We may turn now to another point which arises in connection with positional differentiation.

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*So far as I am able to judge from the present material there is apparently nothing in Ceratophyllum when it grows in this way as a perennial corresponding to the "localized stages" discussed by Jackson ('99), Cushman (:02, :03, and :04), Shull (:05), etc. The new growth in the spring appears to go on in precisely the same manner as it would have if there had been no interruption. This is, of course, what would be expected in a plant like Ceratophyllum. My material at present is not sufficiently great to enable me to make a positive statement that no change whatever in the growth curve takes place at points where new growth of this kind begins. So far, though, I have seen no certain indication of such a change.

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THE CORRELATION BETWEEN DIFFERENTLY SITUATED WHORLS IN RESPECT TO LEAF-NUMBER.

In the preceding section we have examined the correlation existing between leaf-number and position of the whorl on the axis, and in that way determined the law according to which the size of whorls changes with different positions on the branch. We may now consider the further problem of how the absolute sizes of different whorls are correlated together. Especially it is desirable to determine to what degree the first whorl on a branch is correlated with whorls farther out. In this way we shall see whether a particular branch has as a whole a definite tendency or "set" towards a relatively large (or small) absolute leaf-number for all its whorls. It will be seen that this problem is quite distinct from that considered in the last section. We are not now concerned with the law of change with growth, but rather with absolute sizes. All the whorls on a given branch may be relatively large or relatively small and still have been differentiated according to our logarithmic law. The question, then, with which this section has to do may be stated in this way: If the first whorl on a branch has more than the average number of leaves, will the succeeding whorls on the same branch also tend to have in each case more than the average number of leaves for their respective positions? In order to test this question we have to determine individually the correlation between the first and each successive whorl on the branch. On account of lack of material I have not been able to carry the correlations beyond the tenth whorl. For the same reason it is necessary to confine the discussion to primary-branch whorls. We may first examine the results from the data of Series I, II, and III combined. In table 47, page 94, is given the raw material. It may be noticed that the totals of these tables do not agree with those for the corresponding whorls in table 32, because in that table every unmutilated whorl is included, while here we have, of course, been restricted to every unmutilated *pair* of whorls. Naturally, a great many broken whorls pair with unmutilated ones which appear in the earlier tables, but not in these.

The coefficient of correlation was determined for each of these tables in the ordinary way. The values so obtained, together with their probable errors, are given in table 48, page 95.

There is clearly a very distinct correlation between the first and second and first and third whorls. As we go farther out on the branch the correlation steadily decreases, till finally at the ninth whorl it becomes sensibly zero. There is apparently a rise in the correlation at the eighth whorl, but this is probably a purely accidental result arising from the fact that the number of pairs is getting too small to depend

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on for smooth results. The correlations are all positive, with the exception of that for the ninth whorl, which is negative, but so low as to be entirely insignificant in comparison with its probable error. The data from Series IV lead to essentially the same results as the Series I, II, and III material, and consequently it does not seem necessary to take the space to reproduce the figures in detail.

TABLE 47.—*Correlation between the first and each of the following nine whorls on primary branches in respect to leaf-number. Series I, II, and III combined.*

First whorl.	A.—Second whorl.							B.—Third whorl.							C.—Fourth whorl.				
	5	6	7	8	9	10	Total.	6	7	8	9	10	11	Total.	7	8	9	10	Total.
5.....	...	...	1	...	...	...	1	...	...	1	...	...	...	1	...	...	...	...	...
6.....	1	6	17	18	4	...	46	...	8	21	9	...	...	38	4	13	14	...	31
7.....	...	2	16	20	16	2	56	...	5	20	16	2	1	54	4	18	18	3	43
8.....	...	...	5	14	14	3	36	1	...	10	14	7	1	33	...	6	10	10	26
9.....	...	...	...	2	5	1	8	...	...	...	4	1	...	5	1	...	2	2	5
Total..	1	8	39	54	39	6	147	1	13	52	53	10	2	131	9	37	44	15	105

First whorl.	D.—Fifth whorl.							E.—Sixth whorl.					F.—Seventh whorl.						
	6	7	8	9	10	11	Total.	8	9	10	11	Total.	6	7	8	9	10	11	Total.
5.....	...	1	...	...	...	...	1	...	1	...	...	1	...	...	...	...	...	...	...
6.....	...	1	11	16	2	...	30	4	17	1	1	23	1	...	4	10	4	1	20
7.....	1	...	11	19	5	1	37	9	15	8	...	32	...	...	6	12	8	...	26
8.....	1	...	2	12	6	...	21	...	10	6	...	16	...	...	2	5	7	1	15
9.....	...	...	...	2	1	...	3	...	1	2	...	3	...	...	...	2	1	...	3
Total.	2	2	24	49	14	1	92	13	44	17	1	75	1	...	12	29	20	2	64

First whorl.	G.—Eighth whorl.						H.—Ninth whorl.						I.—Tenth whorl.						
	7	8	9	10	11	Total.	7	8	9	10	11	Total.	6	7	8	9	10	11	Total.
6.....	1	3	9	1	...	14	...	3	4	5	...	12	...	...	1	4	6	...	11
7.....	2	2	5	13	...	22	...	2	6	10	1	19	1	1	...	7	5	...	14
8.....	...	1	5	6	1	13	...	...	6	6	...	12	1	...	...	5	5	...	11
9.....	...	...	...	3	...	3	1	...	1	1	...	3	...	...	...	...	2	...	2
Total..	3	6	19	23	1	52	1	5	17	22	1	46	2	1	1	16	18	...	38

We may safely conclude, then, that *there is a distinct tendency for branches which show an excess (or defect) from the average in the number of leaves in the first whorl, to have the succeeding whorls greater (or less) than their respective averages. The longer the branch grows the weaker this tendency becomes, till finally, when the ninth or tenth whorl is reached, the number of leaves which it bears is entirely independent of the number in the first whorl.* Branches which start large maintain an excess over the average for roughly 6 to 8 whorls. So far as our data go they show the same kind of relation for the other axial divisions of the plant, viz,

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a positive correlation between the first few successive whorls, diminishing the farther out we go. The material for investigating the matter in these cases is, however, so meager that it is not worth while to discuss it in detail.

TABLE 48.—*Coefficients of correlation from table 47.*

Correlation between—	r.
First and second whorl	0.456±0.044
First and third whorl	.402± .049
First and fourth whorl	.360± .057
First and fifth whorl	.260± .066
First and sixth whorl	.262± .072
First and seventh whorl	.208± .077
First and eighth whorl	.393± .079
First and ninth whorl	— .007± .099
First and tenth whorl	.002± .109

THE VARIABILITY OF SUCCESSIVELY FORMED WHORLS.—THE SECOND LAW OF GROWTH IN CERATOPHYLLUM.

We come now to the consideration of a matter of very considerable interest and importance in connection with the general laws of morphogenesis in Ceratophyllum. It is as to whether whorls in different positions on the plant show equal degrees of variability. We have seen that the mean leaf-number of successively formed whorls changes in a regular and orderly way. We have now the further problem: Does the *variability* of whorls successively formed similarly show a tendency to orderly change, and if so, what law does this change follow?

In discussing the subject we may adopt the notation and methods used by Pearson (:05) in his memoir on "Skew Correlation." If we let σ_{n_x} denote the standard deviation of an x-array of a character B, and σ_y the total variability of the same character, then (Pearson, loc. cit., p. 10): "A curve in which the ratio of σ_{n_x} to the standard deviation σ_y is plotted to x may be termed a scedastic curve."

Further, Pearson says (p. 22):

> I must remind the reader, however, that the form of the regression line does not in any way limit the nature of the distribution of the array about its mean; the variability of an array, i. e., the standard deviation of an array, having for its mean value $\sigma_y\sqrt{1-\eta^2}$, may or may not be the same for all arrays. If it is the same, or all arrays are *equally scattered* about their means, I shall speak of the system as a *homoscedastic* system, otherwise it is a *heteroscedastic* system.

For every array of the correlation tables for position and leaf-number given above (pp. 59 and 60) I have calculated the ratio $\frac{\sigma_{n_x}}{\sigma_y}$, with the re-

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sults set forth in tables 49 and 50. Lest there should be any misunderstanding as to just what these figures mean, it may be said that each value gives the ratio which the variability of whorls in a designated position on the branch in respect to leaf-number is to the variability of all whorls taken together. We may consider first the primary branches.

TABLE 49.—*Variability of successively formed primary-branch whorls.*

Position of whorl.	Variability in leaf-number, measured by ratio σ_{n_z}/σ_y.						
	Series I.	Series II.	Series III.	Series IV.	Series I, II, III combined.	Series V, all branches.	SeriesIV,all branches.
1	0.867	0.684	0.732	0.855	0.771	1.003	0.908
2	.773	.822	.747	.812	.806	.902	.791
3	.657	.791	.681	.685	.733	.821	.677
4	.722	.639	.657	.698	.712	.761	.750
5	.710	.831	.628	.821	.765	.711	.667
6	.793	.568	.517	.744	.659	.772	.699
7	.836	.678	.616	.629	.749	.793	.614
8	.760	.705	.760	.652	.747	.870	1.099
9	.806	.698	1.085	.700	.826	.667	.512
10	.757	1.023	.378	1.247	.899	.440	.784
11	.651	1.011	.378	.837	.772	.....	.....
12	.775	1.021	.616	.480	.904	.....	.....
13	.841	.653	.411	.449	.736	.....	.....
14	.521	.514	.411	.430	.511	.....	.....
15	.371	.347	0	.298	.352	.....	.....
16	.807	.292	.436	.658	.499	.....	.....
17	.393	.609	.872	.825	.603	.....	.....
18	.624	1.181	.486	.468	.945	.....	.....
19	.361	.692	0	.430	.557	.....	.....
20	.786	.885	0	.467	.686	.....	.....
21	.681	0	0	0	.420	.....	.....
22	.393	0	0	.496	.416	.....	.....
23	0	0	0	0	0	.....	.....
24	.834	.417	0	0	.577	.....	.....
25	0	0	0	.....	0	.....	.....
26	.834	0	0	.....	.626	.....	.....
27	.884	0	0	.....	.727	.....	.....
28	0	0	0	.....	0	.....	.....
29	0	.....	.....	.....	0	.....	.....
30	0	.....	.....	.....	0	.....	.....

Before discussing these results we may examine those for the secondary branches, which are given in table 50.

Even the most superficial examination of the values given in these tables shows us at once that the whorls in different positions on the axis do not form a homoscedastic system. The variability is not the same in whorls occupying different positions. We have now to consider the further question of whether the change in variability as we consider whorls in different positions is entirely irregular, or whether, on the contrary, it follows some definite law, as we have seen to be the case

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with the means. The matter is one of such considerable importance that it will be considered in some detail.

TABLE 50.—*Variability of successively formed secondary-branch whorls.*

Position of whorl.	Variability in leaf-number, measured by ratio σ_n/σ_y				
	Series I.	Series II.	Series III.	Series IV.	Series, I, II, III, combined.
1	0.641	0.684	0.623	0.647	0.655
2	.710	.659	.538	.712	.638
3	.845	.644	.562	.708	.693
4	.800	.422	.579	.727	.582
5	.555	.473	.548	.739	.536
6	.813	.450	.447	.776	.558
7	.705	.368	.467	.682	.476
8	.406	.682	.389	.741	.527
9	.431	0	.686	.610	.623
10	.863	0	.389	.643	.720
11	0	.....	0	.721	0
12	0	.....	0	.266	.376
13	0	.....	.....	.594	0
14	.....	.....	.....	.319	.....
15	.....	.....	.....	0	.....
16	.....	.....	.....	.417	.....
17	.....	.....	.....	0	.....
18	.....	.....	.....	0	.....

Confining our attention at first to the primary branches, I think it reasonably clear that, disregarding minor fluctuations due to the relative smallness of the numbers of observations, there is a tendency for the variability of whorls in leaf-number to decrease, the farther out on the branch we go. The minor fluctuations are, however, rather disturbing, and in order to get clear results we must resort to graphical representation and graduation. In that way we can get an idea of the general trend of the variability, apart from its accidental fluctuations. In order that the diagrams might not be too extended, and that at the same time we might get a sort of "first smooth" of the observations, I have combined the whorls into pairs and taken the weighted means of the ratio $\frac{\sigma_{n_2}}{\sigma_y}$ for each pair. Thus, whorls 1 and 2 have been combined and a weighted mean taken; whorls 3 and 4 combined together, and so on for the whole length of the branch. In taking the means, each single observation was weighted with the frequency in the array from which $\frac{\sigma_{n_2}}{\sigma_y}$ was calculated. Proceeding in this way, we have for Series I, II, and III combined the series of values given in table 51.

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TABLE 51.—*Weighted mean variability of successively formed primary-branch whorls.*

Position.	Mean of σ_{n_x}/σ_y	Position.	Mean of σ_{n_x}/σ_y
Whorls 1 and 2.....	0.788	Whorls 17 and 18.....	0.768
Whorls 3 and 4.....	.723	Whorls 19 and 20.....	.618
Whorls 5 and 6.....	.719	Whorls 21 and 22.....	.418
Whorls 7 and 8.....	.748	Whorls 23 and 24.....	.266
Whorls 9 and 10.....	.864	Whorls 25 and 26.....	.376
Whorls 11 and 12.....	.834	Whorls 27 and 28.....	.415
Whorls 13 and 14.....	.624	Whorls 29 and 30.....	0
Whorls 15 and 16.....	.416		

Even with this slight smoothing it is clear from the figures themselves that the variability is tending to become smaller in the higher whorls, till we finally reach a condition of no variability at the ends of the branches, or in other words, till all the frequency falls on one type of whorl. These data are shown graphically in fig. 17.

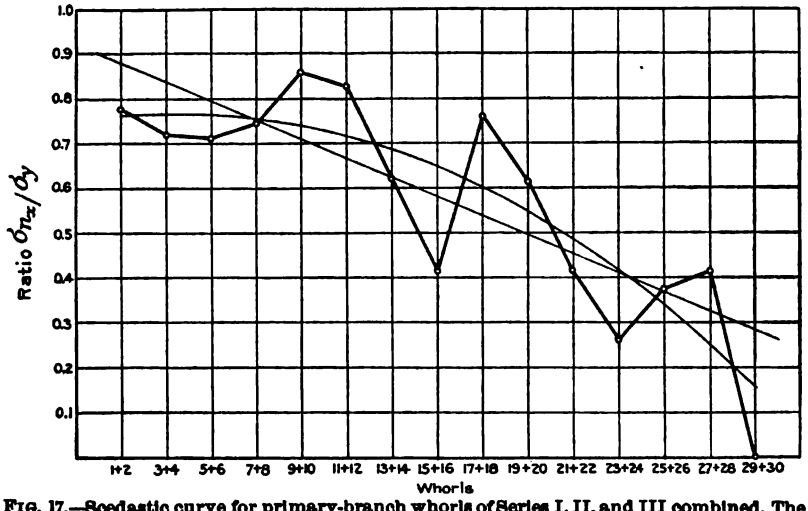

FIG. 17.—Scedastic curve for primary-branch whorls of Series I, II, and III combined. The abscissas give the position of the whorls, and the ordinates the ratio σ_{n_x}/σ_y. o——o, observations. The fitted straight line and parabola are given by continuous lines.

From this diagram it is at once evident that there is a clearly marked and *definite tendency for the variability to decrease with the successive formation of whorls.* Whorls formed when the branch first begins its growth are more variable than those formed later. In order to give a more precise idea of the rate at which this decrease in variability goes on I have fitted to the observations given in fig. 17 a straight line and a parabola. The fitting was very easily done by the method of moments

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(Pearson, :02), using the corrective terms for the moments of trapezia. The equations are as follows:

$$\text{Straight line, } y = 0.5845 \left\{1 - 0.5103 \left(\frac{x}{l}\right)\right\}$$

$$\text{Parabola, } \quad y = 0.5845 \left\{1.1084 - 0.5103 \left(\frac{x}{l}\right) - 0.3249 \left(\frac{x}{l}\right)^2\right\}$$

where y is the ordinate (i. e., the probable value of σ_{n_x}/σ_y) and l, the half range, equals 7 units. In these and all the curves which follow in this section of the paper the origin of x is taken at the central ordinate of the group. Both line and parabola give very reasonable graduations, and until we have much larger numbers than at present it is impossible to say which one gives the truer representation of the scedastic curve for Ceratophyllum. What I wish to bring out now is that when we smooth the observations by a graduation formula there can be no doubt that the general trend of the variability is to decrease as the position of the whorl on the branch, or in other words, the order of its formation, increases.

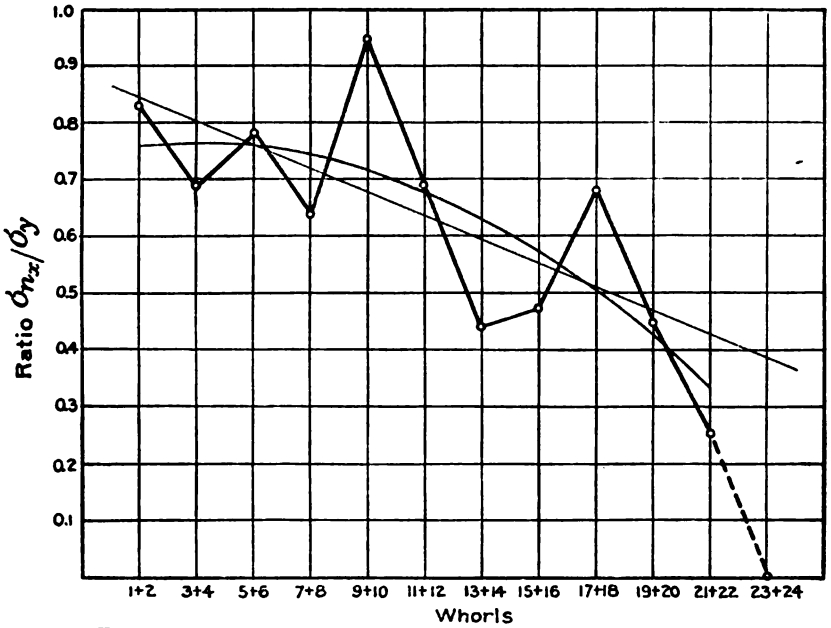

FIG. 18.—Scedastic curves for primary-branch whorls of Series IV. Significance of lines as in fig. 17.

Do the other series show the same relation? Treating the data given in table 49 for primary-branch whorls of Series IV in exactly the same

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way as we have those for Series I, II, and III, we get the results shown in fig. 18. The zigzag line gives the weighted means of the successive pairs of observations given in table 49.

As before, I have fitted a straight line and a parabola to the data. In order to have an odd number of points for the fitting of the constants, the curves were calculated from the first 11 observations ($l = 5$) neglecting the twelfth. Apart from the practical reason, this procedure was theoretically justifiable because of the small number of whorls on which this last observation is based. The equations to the curves are:

$$\text{Straight line, } y = 0.6347 \left\{ 1 - 0.3292 \left(\frac{x}{l}\right) \right\}$$

$$\text{Parabola, } \quad y = 0.6347 \left\{ 1.0701 - 0.3292 \left(\frac{x}{l}\right) - 0.2102 \left(\frac{x}{l}\right) \right\}$$

Again we see that the general trend of the curve is downwards as we pass to the whorls farther out on the branches. The slope of the curve is somewhat more rapid than in the case of Series I, II, and III, but the difference in this respect is not great. We must conclude that here as in the former case the variability decreases with successive whorl formation.

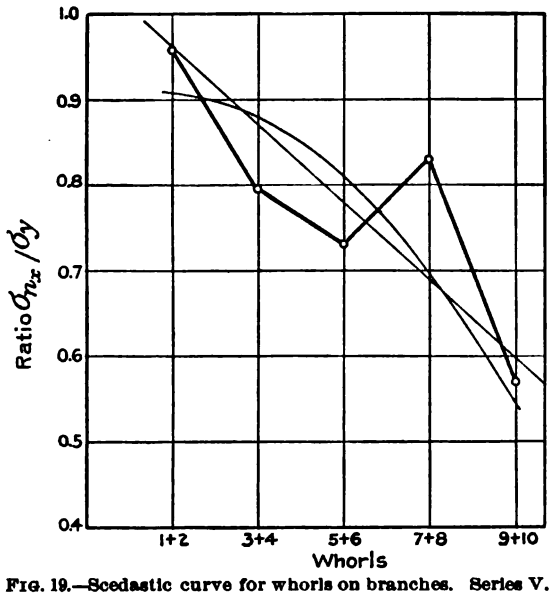

FIG. 19.—Scedastic curve for whorls on branches. Series V. Weighted means of successive pairs. Significance of lines as in fig. 17.

We may next consider Series V and VI. Here it will be recalled that we are dealing not solely with primary-branch whorls, but with all the whorls borne on branches on the plant as a whole. Furthermore, for reasons set forth above (p. 58), we have considered only the first 10 whorls. Dealing with Series V in the same way that we have with the other series (i. e., combining successive whorls in pairs and taking the weighted mean for each pair) we have the result shown in fig. 19.

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The equations to the fitted curves, when $l = 2$, are

Straight line, $y = 0.7812\left\{1 - 0.2297\left(\frac{x}{l}\right)\right\}$

Parabola, $y = 0.7812\left\{1.0338 - 0.2297\left(\frac{x}{l}\right) - 0.1015\left(\frac{x}{l}\right)^2\right\}$

The result is the same as before. There is very clearly a decrease in the variability with successive whorl formation. Since the total number of successive whorls dealt with in this case (only 10) is so small, it is perhaps worth while to examine the results obtained when each whorl is considered by itself instead of being paired with the one following. Fig. 20 shows the result in this case. Here each circle represents the ratio $\frac{\sigma_{n_x}}{\sigma_y}$ for the whorls in the particular position designated by the abscissal number.

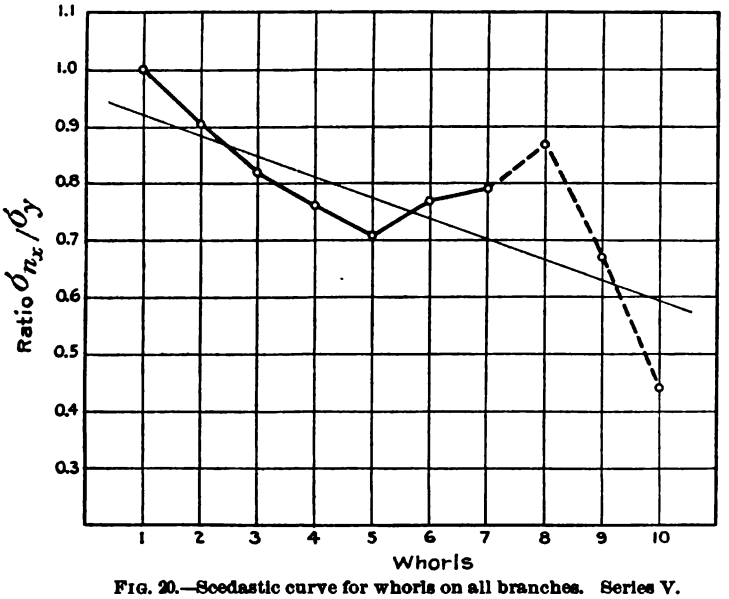

FIG. 20.—Scedastic curve for whorls on all branches. Series V.

In fitting the straight line to the observations in this case I have used only the first seven points. The last three are very irregular, on account of the small number of whorls on which they are based. The equation to the line, where now $l = 3$, is,

$$y = 0.8108\left\{1 - 0.1326\left(\frac{x}{l}\right)\right\}$$

We reach the same result as before, namely, that the variability decreases as we go out on the branch. The smoothness of the scedastic curve for the first five observations in this case is remarkable,

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As shown by fig. 21, Series VI leads to the same conclusion as the other series. In this case each observation is given separately. The straight line was fitted to the first 7 points. As in the case of Series V, the last three observations are based on a small number of whorls, and are in consequence very irregular.

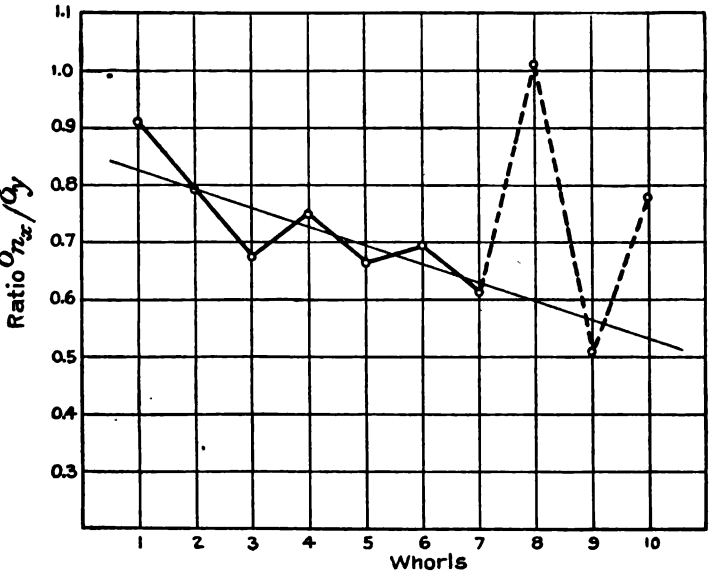

FIG. 21.—Scedastic curve for whorls on all branches. Series VI.

The equation to the straight line, where $l = 3$, is,

$$y = 0.7242\left\{1 - 0.1348\left(\frac{x}{l}\right)\right\}$$

All our series agree, then, in showing that the variability in leaf-number in successively formed whorls on primary branches changes inversely as the order of formation of the whorl. The whorls first formed are the most variable, and the degree of variability steadily diminishes in the later whorls.

We may next consider the question of whether the same relation holds for secondary-branch whorls. It is evident, I think, from an examination of table 50 (p. 97) that such is the case. In order, however, that there may be no doubt about it we may consider in detail the combined data for Series I, II, and III. The data given in the last column of table 50 are plotted in fig. 22. The irregularity in the last four observations is due to small numbers in the arrays here, as will be seen by reference to table 37 (p. 74).

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The equation to the straight line is,

$$y = 0.5054\left\{1 - 0.4442\left(\frac{x}{l}\right)\right\}$$

where $l = 6$. The fit is a very reasonable one, and clearly a straight line gives a sufficiently good graduation for our present purpose, which is merely to show the general trend of the observations. Out as far as the 9th whorl the scedastic curve is quite regular. I think that there can be no doubt that the secondary-branch whorls follow the same law as those on primary branches in respect to their variability. The variation in leaf-number decreases more and more as successive whorls are formed.

FIG. 22.—Scedastic curve for secondary-branch whorls. Series I, II, and III combined.

We may fairly conclude that what is true of the variability of primary and secondary branch whorls will also be true of whorls on other branch divisions of the plant (tertiaries, etc.). On account of the relatively small number of tertiary-branch whorls it is not possible to test the matter directly there. Our results in the previous section of the paper with reference to the mean number of leaves in successive whorls in different divisions of the plant makes it very probable that a similar uniformity prevails with reference to variability.

Fortunately, we can test the matter directly for main-stem whorls. In table 42 (p. 83) are given, for the combined plants of Series I, II,

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and III, the frequency of the various leaf-numbers for successive whorls, proceeding by groups of 10 whorls. Calculating the standard deviation (σ_{n_x}) for each array of this table, and dividing it in each case by the standard deviation (σ_y) of all main-stem whorls, we have the results shown in table 52.

TABLE 52.—*Variability of successive main-stem whorls.*

Position.	Variability.	Position.	Variability.
Whorls 1 to 10.....	1.041	Whorls 51 to 60.....	0.808
Whorls 11 to 20.....	1.190	Whorls 61 to 70.....	.543
Whorls 21 to 30.....	1.110	Whorls 71 to 80.....	.426
Whorls 31 to 40.....	.892	Whorls 81 to 90.....	0
Whorls 41 to 50.....	.843		

The data in this table are shown graphically in fig. 23.

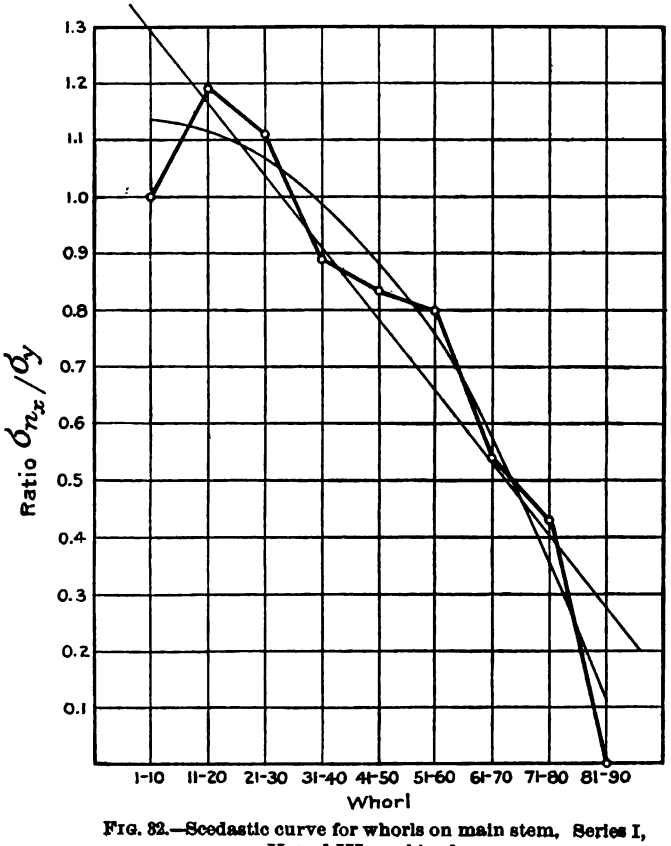

FIG. 32.—Scedastic curve for whorls on main stem, Series I, II, and III combined.

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I have fitted to the observations the following curves:

$$\text{Straight line } y = 0.7903\left\{1 - 0.6428\left(\frac{x}{l}\right)\right\}$$

$$\text{Parabola} \qquad y = 0.7903\left\{1.1096 - 0.6428\left(\frac{x}{l}\right) - 0.3289\left(\frac{x}{l}\right)^2\right\}$$

where $l = 4$.

There can be no doubt that the main-stem whorls show the same decrease in variability which we have observed in the other divisions of the plant. Indeed, the results for the main stem are more regular than for any other of the groups considered. This is of course due to the fact that we have a much larger range of position (1 to 80) and so get a smoothing effect by taking the whorls in groups of 10. In this case it is clear that the parabola gives a somewhat better graduation than does the straight line, but the gain is mainly in the representation of the first and last observations, on neither of which can much weight be laid.

The difficulty with reference to the first observation is that so many of the proximal main-stem whorls were mutilated and could not be counted, thus giving disproportionate weight to the others (cf. p. 83). This would of course operate to lower the variability for that group. The last observation is based on too few whorls to be significant.

So far it has been shown that when the variability of the whorls situated in a definite position on an axial division is measured by taking the ratio of the standard deviation of such whorls to the standard deviation of all whorls on the same axial division, the degree of variability decreases as the distance of the whorl from the proximal end of the branch (or main stem) increases. Now, this measure of variation, consisting as it does of the ratio of two standard deviations, gives no idea of the degree of variability in proportion to the size of the thing varying. It has been shown in a preceding section that the mean leaf-number changes in a very regular and definite way in successive whorls, the direction of this change being an increase in the mean with every increase in the distance of the whorl from a fixed point on the axis.

Since the means thus *increase* with successive whorl formation, while, as we have seen, the absolute variability *decreases*, clearly there must be a still more marked decrease in the relative variability in proportion to the size.

If we take the percentage of the standard deviation to the mean (coefficient of variation) for each array corresponding to a definite posi-

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tion on the axis, we shall clearly have a measure of this relative variability. I have done this for all of the tables, but since it is evident, if in an expression

$$v = \frac{100\sigma}{M}$$

σ is decreasing while M is increasing in value, that v must also decrease, it does not seem worth while reproducing these coefficients in detail. In order to afford some idea of how the actual values run, however, there are given in table 53 the coefficients of variation for the first four whorls on primary branches in Series I, II, and III and IV, and on all branches in Series V and VI.

TABLE 53.—*Coefficients of variation for successive whorls of primary branches.*

Position of whorl.	Coefficients of variation.						
	Series I.	Series II.	Series III.	Series IV.	Series I, II, III combined.	Series V, all branches.	Series VI, all branches.
1.....	14.74	11.67	12.00	11.57	13.07	20.54	16.70
2.....	11.77	12.23	10.67	9.68	11.92	16.87	12.56
3.....	9.50	11.15	8.95	7.92	10.31	14.90	9.88
4.....	10.16	8.93	8.73	7.82	9.91	13.29	10.91

We see in all the series that while the branches start with a relatively very variable first whorl, the variability rapidly decreases in the succeeding ones. The same thing is shown if we calculate the coefficients of variation for secondary-branch whorls.

SUMMARY OF SECTION.

In this section of the paper it has been shown that both absolutely and in proportion to the size the variability of successive whorls in respect to leaf-number diminishes as we pass from the most proximal to the most distal whorl on an axial division. This relation has been demonstrated for the three most important axial divisions (main stem, primary and secondary branches), and it can not reasonably be doubted that it also holds in the same way for the other divisions (tertiary and quaternary branches). But from the method of growth of Ceratophyllum we know that succession of whorls in position on the branch denotes succession in order of formation or differentiation from the growing bud. Our result, then, means that *as whorls are successively produced by a growing bud, they are formed with ever-increasing constancy to their type, the ultimate limit towards which the process is tending being absolute constancy.* This may be designated as the "Second law of growth" in Ceratophyllum.

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The operation of this law is to be seen in other of the morphogenetic activities of the plant than those which have been discussed in this section. In a later section data are given showing that it holds in branch production. It seems to me that a number of results obtained earlier in the paper can best be interpreted as due to the operation of this law. Thus, in examining the data on which our first law of growth was based it was found that the slope of the positional regression line was steepest for secondary-branch whorls, less steep for whorls on primaries, and had the least slope in the case of main-stem whorls. It was pointed out in the discussion that this meant that a given type was attained with the production of fewer whorls in secondary than in primary branches, etc. Similarly it appears probable that the diminution in variability with successive whorl formation goes on more rapidly the farther distad on the plant we go. That is, the same rule appears to hold between different axial divisions of the plant as holds for the organs within a given division. In other words, as we go towards the periphery of the plant the variability of repeated characters diminishes in such a manner as to give the impression that in some way there is stored up in the protoplasm, as it were, the results of previous morphogenetic experience. An axillary bud on a primary branch goes through the same series of events when it develops into a branch as does an axillary bud on the main stem. It produces whorls whose type changes according to a logarithmic law, and whose variability diminishes with successive formations. But the rate at which it attains any given result in this series is greatly accelerated over that at which affairs went on in the case of the bud on the main stem. The formative activities of each bud on the plant appear to be influenced in some very direct way by the sum total of previous morphogenetic history of the portion of the plant proximal to the bud. That the two things are objectively related is a fact clearly demonstrated by the results which have been presented in this and earlier sections of the paper. No one who will take the trouble to study carefully these results can fail to be impressed with the reality of the fact, I think. How such a relation as that of which we are speaking is to be interpreted or explained is another question to which we shall return in the concluding section of this paper.

The relation of this second law of growth to our earlier results on the variation in whorls on different axial divisions of the plant is so obvious as hardly to need special mention. In connection with the first law of growth it enables us to interpret very clearly and completely the results regarding variation obtained from grouped material. Thus, for example, it was found that main-stem whorls as a class are least varia-

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ble; primary-branch whorls are more variable; a maximum of variability is reached in secondary-branch whorls as a class; and in tertiary and quaternary whorls the variability tends to decline. It is obvious that the variation shown by any composite group of whorls will depend on two factors: (*a*) the real variability of the whorls in a given position, and (*b*) the mixing of whorls of differentiated types (i. e., whorls which occur at different positions). Now, in the case of main-stem whorls as a class the effects of both *a* and *b* are at the minimum as a result respectively of the operation of our second and first growth laws. In primary-branch whorls the effect of the factor *b* is greater than in the main stem, but since many primary branches are very long the influence of the law of diminishing variability comes in through *a* to keep down the variation exhibited by the group as a whole. When we come to secondary-branch whorls this lowering of the variation through the presence of long branches with many whorls of low variability no longer occurs, because there are few or no long branches. Finally, the drop in the variability shown by tertiary-branch whorls as a class is clearly due to the fact that owing to the extreme shortness of these branches factor *b* contributes very little to the sum total, but instead we have the expression practically of *a* alone.

In following sections of the paper the operation of the law of diminishing variability in other phenomena than whorl production will be discussed. A discussion of its theoretical bearings and interpretation will also be undertaken later in the paper. It need only be pointed out here that it is merely a special case of a much more general biological law applying to other phenomena besides those of growth. Jennings (:05) in a recent paper has enunciated what is essentially the same law in the field of behavior in the following terms: "The resolution of one physiological state into another becomes easier and more rapid after it has taken place one or more times."

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THE RELATION OF THE PRESENCE OF BRANCHES TO THE NUMBER OF LEAVES IN THE WHORL.

The lateral branches in Ceratophyllum always originate of course at nodes, and hence in each case a branch comes into very close relation with the whorl at that node. It seemed desirable to determine whether the presence of a branch at a node in any way influenced the number of leaves in the whorl belonging to that node. To this end frequency distributions were formed for each plant and series, giving the leaf-number in every whorl at which a branch originated. These distributions are given in table 54.

TABLE 54.—*Frequency distributions for leaf-number in whorls at which branches originate.*

Series.	Plant.	Distribution number.	Leaves per whorl.									
			4	5	6	7	8	9	10	11	12	Total.
I	1	37	...	...	...	...	2	13	29	...	...	44
	2	38	...	...	2	1	5	12	13	...	...	33
	3	39	...	...	...	1	8	13	14	2	1	39
	4	40	...	...	...	3	16	27	25	2	...	73
	5	41	...	...	3	1	4	8	7	2	...	25
	All plants	42	...	...	5	6	35	73	88	6	1	214
II	1	57	...	...	1	8	27	65	88	14	...	203
	2	58	...	...	...	5	13	38	53	5	...	114
	All plants	59	...	...	1	13	40	103	141	19	...	317
III	1	71	...	...	4	12	47	109	113	6	...	291
IV	1	92	...	...	...	3	22	88	115	2	...	230
	2	93	...	...	2	11	39	140	193	...	...	385
	All plants	94	...	...	2	14	61	228	308	2	...	615
V	1	130	2	8	4	10	12	19	26	3	...	84
	2	131	...	...	...	1	...	1	2	...	...	4
	3	132	...	...	...	...	1	2	7	...	...	10
	4	133	...	...	...	...	...	6	...	...	...	6
	5	134	...	...	...	1	...	5	5	...	...	11
	6	135	...	...	2	2	5	7	3	...	...	19
	7	136	...	...	2	7	3	18	8	...	...	38
	All plants	137	2	8	8	21	21	58	51	3	...	172
VI	1	168	...	...	1	4	2	8	7	...	...	22
	2	169	...	...	1	1	5	10	5	...	...	22
	3	170	...	...	...	...	3	2	4	...	...	9
	4	171	...	...	...	4	1	4	5	1	...	15
	5	172	...	1	1	4	4	15	42	...	...	67
	6	173	...	...	...	2	5	4	29	6	...	46
	All plants	174	...	1	3	15	20	43	92	7	...	181

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We note at once from this table that the most frequently occurring whorls at the nodes where branches originate are those having 10 leaves (with the single exception of Series V, in which the 9 and 10 leaved whorls are approximately equally frequent). Further, it appears that generally whorls having a small number of leaves do not occur at the origin of branches, though there are individual exceptions.

The constants for the largest of these distributions are given in table 55.

TABLE 55.—*Constants for variation in leaf-number in whorls at which branches originate.*

[Unit — 1 leaf.]

Series.	Plant.	Distribution number.	Mean.	Standard deviation.	Coefficient of variation.
I	1	37	9.614±0.058	0.573±0.041	5.957±0.430
	2	38	9.000± .129	1.101± .091	12.233±1.031
	3	39	9.282± .109	1.011± .077	10.897± .842
	4	40	9.096± .072	.909± .051	9.994± .563
	5	41	8.840± .189	1.405± .134	15.895±1.554
	All plants	42	9.192± .046	1.007± .033	10.959± .362
II	1	57	9.345± .046	.962± .032	10.294± .348
	2	58	9.351± .057	.898± .040	9.605± .433
	All plants	59	9.347± .036	.940± .025	10.052± .272
III	1	71	9.144± .038	.949± .026	10.375± .293
IV	1	92	9.396± .032	.725± .023	7.720± .244
	2	93	9.327± .028	.810± .020	8.687± .213
	All plants	94	9.353± .021	.780± .015	8.343± .162
V	1	130	8.357± .132	1.790± .093	21.424±1.165
	7	136	8.605± .127	1.159± .090	13.473±1.061
	All plants	137	8.581± .077	1.502± .055	17.499± .655
VI	2	169	8.773± .143	.997± .101	11.364±1.170
	5	172	9.343± .090	1.086± .063	11.630± .687
	6	173	9.696± .097	.975± .069	10.057± .714
	All plants	174	9.238± .057	1.134± .040	12.277± .442

From this table the following points are to be noted:

(*a*) The mean number of leaves in the whorls where branches start is relatively high. If we compare the values given in this table with those for the different axial divisions of the plant presented earlier in the paper (tables 6, 13, 15, 18, 23, and 24) we see that these whorls agree more closely in type with those borne on the main stem than with any others.

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(*b*) The variabilities, both absolute and relative, shown in this table are comparatively low. Again they agree most closely with what has been found for main-stem whorls.

We get the same results, only still more marked, if we consider the whorls at nodes where two branches originate. This "double" branching at one node does not occur very commonly in Ceratophyllum according to our experience, but in one plant (No. 2, Series IV) such cases were especially abundant. Table 56 shows the condition, in respect to leaf-number, of these whorls on the plant mentioned.

TABLE 56.—*Frequency distribution for variation in leaf-number of whorls where two branches originate. Plant 2, Series IV.*

	Leaves per whorl.				
	7	8	9	10	Total.
Frequency.....	1	2	41	120	164

The constants for this distribution are as follows:

Mean	$= 9.707 \pm 0.027$
Standard deviation	$= .518 \pm .019$
Coefficient of variation	$= 5.333 \pm .199$

Comparing these with the values in table 55 for the same plant we see that there is a still further raising of the mean and lowering of the variability in the whorls at which two branches start.

Now the question arises, can we consider the relatively high mean and low variability of these whorls at which branches originate to be a specific result of the presence of one or more branches at the node to which the whorl belongs? Clearly, without further evidence, we can not, because of the fact that among these whorls some are borne on the main stem, others on primary branches, and still others on secondary branches, and it has been shown that whorls are differentiated in respect to leaf-number according to the part of the plant on which they are borne. Further, according to the two laws of growth which have been set forth above, it is clear that the number of leaves in whorls from which branches originate will depend, in part at least, on the position which such whorls occupy on their axes. Before we can reach conclusions as to whether the presence of a branch influences the number of leaves in the whorl we must determine the probable condition of such whorls as a result merely of the operation of the usual laws of growth. If, then, it be found that these whorls differ considerably from the condition of "whorls in general" occupying the same relative position on the

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plant, it may safely be concluded that the branching exercises a specific influence.

In order to test this matter it is necessary to know first of all something about the positions at which branches originate. Is the chance of a branch occurring the same for all nodes? Or is branching more abundant in some positions on the axes of the plant than in others? To answer these questions the frequency of occurrence of branches at the different nodes must be determined. This has been done for the secondary branches of the first four series, with the results shown in table 57. The way in which the table was made was to enter for each plant the number of secondary branches which originated at specified nodes on primary branches, the nodes being numbered in order, beginning with 1 as the most proximal. In case two secondaries arose at the same node each was entered separately.

TABLE 57.—*Frequency distributions showing position of secondary branches.*

Position.	Frequency of secondary branches.													
	Series I.						Series II.			Series III.	Series I, II, III.	Series IV.		
	Plant.					Total.	Plant.		Total.	Plant 1	All plants.	Plant.		Total.
	1	2	3	4	5		1	2				1	2	
1	1	...	3	2	3	9	13	3	16	9	34	7	13	20
2	1	...	2	3	...	6	7	6	13	13	32	5	11	16
3	1	...	2	5	4	12	15	6	21	23	56	14	29	43
4	1	4	2	3	...	10	12	6	18	15	43	9	33	42
5	1	...	1	2	1	5	11	2	13	13	31	12	27	39
6	2	...	1	2	1	6	12	4	16	12	34	12	31	43
7	1	1	2	4	2	10	6	4	10	9	29	12	28	40
8	...	...	1	2	...	3	4	4	8	4	15	9	26	35
9	1	1	1	1	...	4	4	4	8	3	15	8	22	30
10	1	3	1	6	1	12	5	3	8	3	23	7	20	27
11	3	...	...	1	3	7	2	3	5	4	16	4	19	23
12	1	1	...	...	...	2	2	2	4	3	9	5	15	20
13	2	1	...	2	1	6	2	2	4	1	11	5	13	18
14	...	3	...	1	...	4	2	4	6	3	13	4	10	14
15	...	...	...	...	...	...	...	4	4	1	5	5	9	14
16	2	1	...	...	...	3	1	4	5	2	10	6	7	13
17	2	2	...	1	...	5	1	2	3	2	10	6	4	10
18	1	1	...	...	...	2	1	3	4	1	7	5	5	10
19	...	...	...	1	...	1	1	1	2	3	6	6	...	6
20	...	1	...	1	...	2	1	1	2	3	7	4	2	6
21	...	...	...	1	...	1	1	1	2	1	4	2	2	4
22	...	1	...	1	...	2	2	1	3	3	8	1	2	3
23	...	...	...	1	...	1	1	2	3	1	5	...	2	2
24	...	...	...	1	...	1	2	2	4	1	6	...	...	...
25	...	...	...	...	...	...	1	1	2	1	3	...	...	...
26	...	...	...	2	...	2	...	1	1	2	5	...	...	...
27	...	...	...	1	...	1	...	...	...	1	2	...	...	...
28	...	...	...	1	...	1	...	...	...	1	2	...	...	...
Total	21	20	16	45	16	118	109	76	185	138	441	148	330	478

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Calculating from this table the mean and median positions of secondary branches, we get the results set forth in table 58.

TABLE 58.—*Constants for position of secondary branches. Totals for series.*

Series.	Mean.	Median.
I	9.24	8.33
II	8.39	6.72
III	7.75	5.69
I, II, and III combined	8.42	6.72
IV	8.42	7.90

From these data we see that:

(1) The average position of origin of secondary branches is at roughly the 7th to 9th node from the proximal end of primary branches.

(2) Fifty per cent of all secondary branches originate from the seventh (*ca.*) or more distal nodes of primaries.

(3) There is very close agreement between the different series in respect to the point of origin of secondaries. The mean for the combined Carp Lake material agrees to the third place of figures with that for the Ann Arbor material (Series IV).

From these results it is clear that branches (*a*) do not occur with equal frequency at all nodes, nor (*b*) as will be seen by comparison with tables 26 and 27 (pp. 50, 51), can the positional distributions of branch origins be regarded as random samples of the positional distributions of "whorls in general." Instead it is found that the branches are so distributed in their points of origin that the great majority occur beyond the first few proximal nodes. But it has been seen in what has gone before that (*a*) taking all whorls on branches together there are in the total more first whorls than second, more second than third, and so on (cf. tables 30, 31, and 32, pp. 59 and 60); and (*b*) that the mean number of leaves per whorl is lowest for first whorls and increases as we go in a distal direction. That is to say, the frequency distributions for "whorls in general" contain a higher proportion of whorls which, owing to the operation of our first law of growth, have a small number of leaves than do the distributions for whorls at which branches originate. Naturally, then, we should expect the means to be higher for the latter than for the former distributions. Again, we have seen that distal whorls are less variable than proximal, and that further, the whorls at which branches originate include a higher proportion of distal ones than do the distributions for the entire plants. So we should expect them to be less variable. While it is thus clear that the ordinary growth factors account for a considerable part of the results which have been found for the "branch-origin"

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whorls, we have yet to determine whether the whole effect is to be explained in this way. To test this we have to answer the following question: Is there a sensible difference between the means and variabilities of (*a*) whorls at the nodes where branches originate, and (*b*) an equally large sample of *similarly situated* whorls taken without reference to the presence of branches? An approximate answer to this question can be obtained by the use of our growth equation (I) and the data provided in table 58. If in the equation

$$Y = 7.9520 + 1.3608 \log (x - 0.8015)$$

we substitute for x the values for the mean position of "branch origin" whorls in the different series given in table 58, and solve for Y, we shall get the probable mean leaf-number in a group of primary-branch whorls situated in the same average position on the axis as are the whorls where secondary branches originate. But in the distributions for "branch-origin" whorls all parts of the plant have been included, and not merely primary branches. Consequently the predicted means from the equation will not be strictly comparable with the observed means in table 55. It is to be expected, however, that if the means for whorls where branches originate were calculated for primary branches alone they would not differ greatly from the values given in table 55. This seems probable from the fact that the two other portions of the plant besides primary branches which contribute most largely to the table 55 means are the main stem and secondary branches. But since, as has been shown above (p. 31), main-stem whorls have a relatively high leaf-number, while on the other hand secondary-branch whorls have a low leaf-number (cf. p. 41), owing to the high proportion of proximal whorls, it may fairly be supposed that the effect of these two portions of the plant will about balance each other in the means given in table 55. That this supposition is in fact a reasonable one is shown by the results which follow.

In table 59 are given in parallel columns the observed mean leaf-number in whorls at nodes where branches originate and the predicted leaf-number from equation I, where x takes successively the mean values given in table 58 for Series I, II, III, and IV.

The agreement between observation and prediction is closer than probably would have been expected. The table shows that at the outside not more than 0.2 leaf in the excess of the means for "branch-origin" whorls over "whorls in general" can be due to the combined effect of (*a*) any hypothetical influence of the presence of a branch at the node to which a whorl belongs, and (*b*) the inclusion in our observed means of main-stem and secondary-branch whorls. In Series I the predicted

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value is actually slightly in excess of the observed. In the other three series the small excess of the observed mean is entirely due, I believe, to the fact that in their influence the main-stem and secondary-branch whorls do not exactly balance each other, but on the contrary the main stem preponderates. It has been shown above (table 25, p. 49) that the number of primary branches greatly exceeds the number of tertiaries.

TABLE 59.—*Observed and predicted leaf-number in "branch-origin" whorls.*

Series.	Observed mean.	Predicted mean.	Difference.
I	9.192	9.212	+0.020
II	9.347	9.150	— .197
III	9.144	9.098	— .046
IV	9.353	9.152	— .201

Every primary branch means, of course, an entry of one main-stem whorl in the frequency distributions of table 54, while every tertiary branch means the entry of one secondary-branch whorl (excepting, naturally, in both cases mutilated whorls). Hence if primary branches exceed tertiaries in number we should expect a preponderant effect of main-stem whorls (with high leaf-number) over secondary-branch whorls (with low leaf-number) in the means of table 55.

Taking all these points into account I think we may safely conclude that *the presence of a branch originating at a particular node is without any influence on the number of leaves in the whorl belonging to that node.* This conclusion is confirmed by the data for whorls at which two branches originate, but it hardly seems worth while reproducing the evidence in detail. Strasburger (:02) states that the same thing is true with regard to the influence of flowers on the leaf-number in whorls. He says (p. 486): "Die in einem Wirtel vertretenen Blüthen beeinflussen nicht die Zahl der Blätter."

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THE POSITION OF BRANCHES.

In the last section the ordinal position with reference to the proximal end of the axis of the nodes at which lateral branches originate was studied in order to get light on another question. I wish now to consider on its own account some other phases of the problem of branch production.

The first question which we may consider is as to where, on any given axis of the plant, branches begin. That is, at what node, counting from the proximal end of an axis, does the most proximal branch on that axis appear. And what degree of variation is there in this matter? The frequency distributions giving data on the point for Series I to IV are exhibited in table 60. The data are for the position of the most proximal *secondary* branches.

TABLE 60.—*Frequency distribution for positions of first[a] branches (secondaries).*

Node of primary branch at which the first secondary branch develops.	Frequency of "first" secondary branches.				
	Series I.	Series II.	Series III.	Series I, II and III combined.	Series IV.
1	9	12	8	29	21
2	2	9	7	18	7
3	4	10	7	21	20
4	6	4	2	12	12
5	2	...	...	2	6
6	3	1	...	4	...
7	3	2	1	6	...
8	...	...	...	...	1
9	1	2	...	3	...
10	...	...	...	...	1
11	2	...	...	2	...
12	1	...	...	1	...
13–18	...	...	...	...	...
19	1	...	...	1	...
Total	34	40	25	99	68

[a] Throughout the section of the paper the most proximal branch on any axis of the plant will be designated as a "first" branch, the next branch distad of this as the "second" branch, and so on. (Cf. fig. 25, *infra*.)

Calculating from this table I find for the means, medians, and standard deviations the following values:

TABLE 61.—*Constants for variation in position of "first" secondary branches.*

Series.	Mean.	Median.	Standard deviation.
I	4.71	4.33	3.94
II	2.85	2.89	2.08
III	2.32	2.64	1.35
I, II, and III combined	3.35±0.20	3.12	2.92±0.14
IV	2.81± .15	3.30	1.84± .11

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TABLE 62.—*Frequency distributions for position of the first five secondary branches. Series I, II, and III combined, and Series IV.*

SERIES I, II, AND III COMBINED.

Node of primary branch at which secondary originates.	First secondary branch.	Second secondary branch.	Third secondary branch.	Fourth secondary branch.	Fifth secondary branch.
1	29	...	...	...	...
2	18	14	...	...	...
3	21	16	12	...	...
4	12	12	11	7	...
5	2	6	10	11	3
6	4	7	5	7	9
7	6	2	4	5	5
8	...	2	1	2	4
9	3	1	...	1	2
10	...	5	2	1	1
11	2	1	2	2	1
12	1	...	...	2	...
13	...	...	2	...	3
14	...	...	...	1	...
15 and 16	...	...	...	...	...
17	...	1	...	...	1
18	...	...	...	...	...
19	1	...	...	...	...
20	...	...	1	...	...
21	...	...	...	1	...
22	...	1	...	...	...
23	...	...	1	...	...
24	...	...	...	...	1
25	...	...	...	...	...
26	...	...	...	1	...
Total	99	68	51	41	30

SERIES IV.

1	21	...	...	...	...
2	7	9	...	...	...
3	20	11	7	...	...
4	12	11	9	4	...
5	6	7	8	7	3
6	...	7	10	8	6
7	...	4	4	9	7
8	1	1	1	4	3
9	...	...	...	...	6
10	1	...	...	...	1
11	...	1	...	...	...
12	...	...	1	...	...
13	...	...	...	1	...
Total	68	51	40	33	26

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TABLE 63.—*Constants for position of secondary branches.*

[Unit = 1 node.]

Series.	Branch.	Mean.	Standard deviation	Series.	Branch.	Mean.	Standard deviation
I, II and III combined.	First.....	3.35	2.92	IV	First.....	2.81	1.84
	Second.....	4.93	4.04		Second.....	4.29	1.87
	Third.....	6.02	4.05		Third.....	5.12	1.73
	Fourth.....	7.37	3.37		Fourth.....	6.27	1.69
	Fifth.....	8.50	4.03		Fifth.....	7.23	1.42

From tables 60 and 61 the following points may be noted:

(*a*) The first secondary branch does not usually occur at the first node of the primary branch. The average position of first branches is at about the third node.

(*b*) Roughly speaking, about 50 per cent of first secondary branches arise at or below (i. e., proximad of) the third node of primaries, and 50 per cent at or above (distad of) this node.

(*c*) There is a close agreement between all the series in respect to the position of origin of secondary branches.

(*d*) There is a wider range and higher degree of variation in this character than would have probably been predicted. Series I is very remarkable in this respect, there being one first branch occurring on the 19th node of the primary axis. All the series had first branches occurring as far out as the 9th or 10th node.

(*e*) In table 60 it is to be noticed that there is apparently a tendency for first branches to occur more frequently at odd than at even nodes, at least at the beginning of the primary axis. In all the series (except III, where the numbers are small) there is a high frequency at the first node, a decided drop at the second node, and a more or less considerable rise again at the third. Beyond this point the numbers are so small that one can not make a safe judgment. So far as the data go it of course looks as if we might possibly have the start of a Fibonacci series here, but there is no evidence whatever of a relatively high frequency at the 5th and 8th whorls as compared with the 4th, 6th, and 7th, which we should expect to find if we were really dealing with such a series.

Having seen how the position of origin of first branches is distributed on the axis from which they spring, we may examine into the same matter in the case of the succeeding branches (second, third, fourth, and fifth). It is not worth while to go beyond the fifth on account of the small number of observations. The data are given in table 62.

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The means and standard deviations for these distributions are given in table 63. It is seen from these tables that:

(*a*) In mean position successive branches are roughly one node apart. This is of course the result we should expect to get if a branch were formed at every node. But while the latter is far from being the case in detail, the branches are so distributed as to give an average result of much the same kind. The regularity of the increase in mean position is shown in fig. 24.

(*b*) Neither the mean nor the modal position of the branches falls at the node we should expect if a branch occurred at each node. Thus first branches occur on the average at the third node, instead of the first, fifth branches at the seventh or eighth node instead of the fifth, and so on. In the case of the Series IV plants the mean position of the branches is quite uniformly two nodes in advance.

(*c*) Each of the first five branches shows about the same degree of variation in its position. In the Series IV plants the variation apparently decreases somewhat in the branches beyond the second, but the differences are so small that no stress can be laid on them.

(*d*) The tendency for branches to occur at odd nodes with greater frequency than at even, which was observed in the case of the first branches, does not appear to hold for other branches, nor beyond the third node.

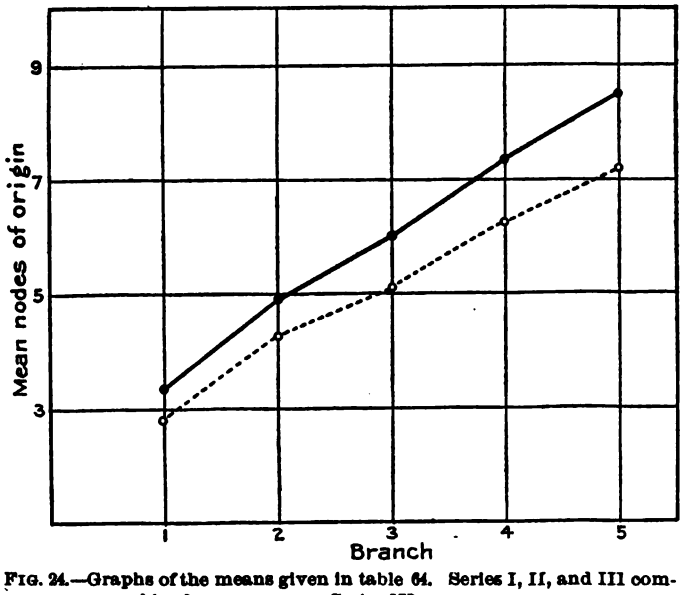

FIG. 24.—Graphs of the means given in table 64. Series I, II, and III combined, ●———; Series IV, ○- - - -.

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We may turn now to another question with reference to the distribution of branches, which may be put in this way: What proportion of first branches have their succeeding (i. e., second) branch on the node immediately distad of that on which they themselves are borne, and in what proportion of cases are there one or more nodes without branches intervening between the two? Similarly, what are the proportions of cases for second and third, third and fourth, etc., branches, where successive branches are borne on contiguous nodes? The data on these questions have been extracted for the first to the sixth secondary branches in the first four series and are shown in table 64. In this table a double column is given to each series, one half being headed + (plus) and the other half — (minus). Whenever the succeeding branch to the one designated in the first (left-hand) column of the table was borne on the next node it was entered in the + (plus) column. When branchless nodes intervened between the two an entry was made in the — (minus) column. Unless at least three whorls of leaves were formed beyond a branch no record was made regarding it. That is, only cases were included where it was possible for a succeeding branch to have been formed.

TABLE 64.—*Position of succeeding branches (secondary).*

Branch.	Proportionate frequency of occurrence of the succeeding branch at the next node.									
	Series I.		Series II.		Series III.		Series I, II and III combined		Series IV	
	+	—	+	—	+	—	+	—	+	—
First	8	23	23	25	18	7	49	55	31	30
Second	7	10	21	8	16	2	44	20	30	17
Third	5	7	13	5	12	4	30	16	27	11
Fourth	4	5	9	5	7	3	20	13	18	11
Fifth	4	3	11	2	3	2	18	7	20	2
Sixth	6	1	7	2	5	0	18	3	19	0

This table shows that there is a decided difference between first branches and those farther distad on the axis, in respect to the matter under consideration. Thus we see that there is more than an even chance that one or more branchless nodes will follow the first branch, while for all the others the chance of a succeeding branch occurring on the next node is greater than the chance that it will not so occur. Further, this chance increases the farther out on the axis we go. This is shown most clearly if we calculate the percentage (in the total number) of the cases in which the immediately succeeding branch occurs at the next node. This has been done for the last two columns of the table (Series I, II, and III combined and Series IV), with the results shown

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in table 65. It will be understood that the figures in this table are the percentages which the + (plus) entries in table 64 are of the sum of the + (plus) and − (minus) entries for each branch.

TABLE 65.—*Percentage of cases in which succeeding branch occurs at the next node.*

Branch.	Series I, II and III combined.	Series IV.	Branch.	Series I, II and III combined.	Series IV.
First	47.1	50.8	Fourth	66.7	62.1
Second	68.8	63.8	Fifth	75.0	90.9
Third	65.2	71.0	Sixth	85.7	100.0

These results speak for themselves. They show that the branch production becomes more regular and orderly the farther out on an axis we go. As the plant grows it tends with ever-increasing certainty to produce a branch at each node. After a time it does this with very remarkable—almost perfect—precision.

TABLE 66.—*Frequency distribution for the occurrence of secondary branches.*

Branch.	Number of branches in 5 nodes following designated branch.											
	Series I, II, and III combined.						Series IV.					
	0	1	2	3	4	5	0	1	2	3	4	5
First	10	7	6	6	11	6	3	5	4	12	5	11
Second	2	1	6	5	7	7	...	1	3	4	5	11
Third	...	1	4	1	5	5	...	...	...	4	3	9
Fourth	...	...	2	4	6	2	...	...	...	2	3	10
Fifth	...	...	1	4	5	2	...	...	...	2	2	9
Sixth	...	...	1	1	3	2	...	...	...	2	1	9
Seventh	...	...	...	...	2	3	...	...	1	2	...	8
Eighth	...	...	...	1	2	2	...	...	1	1	1	5
Ninth	...	...	...	...	1	3	...	...	...	1	1	3
Tenth	...	...	...	...	1	3	...	...	...	...	...	4

The fact that the tendency towards the production of a branch at every node increases the farther distad on the axis we go is brought out in another way by the data given in tables 66 and 67. In these tables are given distributions showing the frequency with which different numbers of branches occur in the five nodes immediately following any designated branch. Thus, considering the portion of a plant diagrammatically represented in fig. 25, in which *ab* is a portion of a main stem, say, and *xy* a primary branch bearing secondaries I to X, we see that in the five nodes following the first branch only one branch occurs. Similarly in the 5 nodes immediately following the second branch only one occurs. In the 5 nodes immediately following *a*, the third, there are 3 branches; *b*, the fourth, there are 4 branches; *c*, the fifth, there

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are 4 branches, etc. Clearly the maximum number of branches possible is 5. Proceeding in the way just illustrated for the first 10 secondary branches on all plants of Series I, II, III, and IV, the results shown in table 66 were obtained. No branch was counted which did not have at least 7 whorls distad of it on the primary axis.

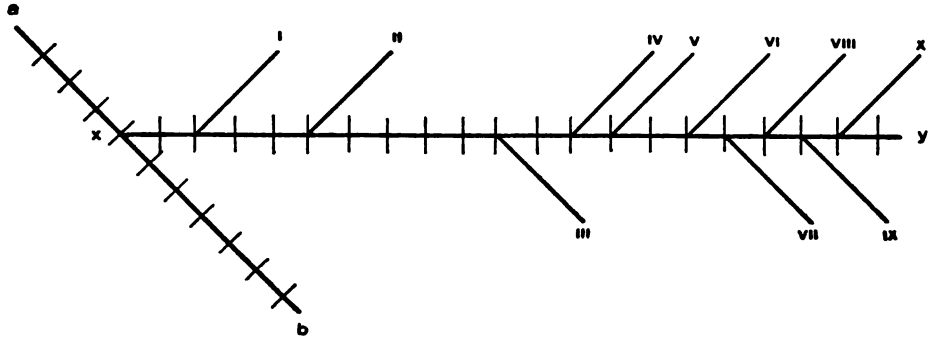

FIG. 25.—Diagram of a portion of a plant. I, "first" branch; II "second" branch; III, "third" branch etc. These secondaries are for convenience represented without leaves. Further explanation in the text.

We see at once from the table that the more distad the branch with which we are dealing lies the larger is the number of branches occurring in the next 5 nodes. When we get beyond the sixth branch less than four occur very rarely. These tables show very plainly the gradual approach towards a condition where each node bears a branch. It will help to make the point still clearer if we examine the means of the arrays in table 67.

TABLE 67.—*Mean number of branches in the five nodes immediately following a designated branch.*

Branch.	Series I, II, and III combined.	Series IV.	Branch.	Series I, II, and III combined.	Series IV.
First	2.41	3.10	Sixth	3.86	4.58
Second	3.25	3.92	Seventh	4.60	4.36
Third	3.56	4.31	Eighth	4.20	4.25
Fourth	3.57	4.53	Ninth	4.75	4.40
Fifth	3.67	4.54	Tenth	4.75	5.00

The increase in the mean number of branches is evident. A little inspection shows, however, that this increase is not uniform in all parts of the table, but is on the whole distinctly more rapid in the first few branches than in the later ones. In other words, the increment in the character under discussion becomes smaller and smaller for the successive branches. This at once suggested that the law of change here might

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be a logarithmic one, similar to what we have previously demonstrated for the growth of leaves. Accordingly the data of this table were fitted with logarithmic curves of the type used in the previous cases, by the same method. The resulting equations were,

Series I, II, and III combined, $Y = 2.4061 + 2.2194 \log x$ . . . . . (I)
Series IV, $Y = 3.8440 + .8931 \log (x - .8)$ . . (II)

in which Y denotes mean number of branches occurring in the five nodes immediately following any designated branch, the ordinal position of which is given by x. Calculating the values of Y for values of x from 1 to 10 we have the results shown in fig. 26.

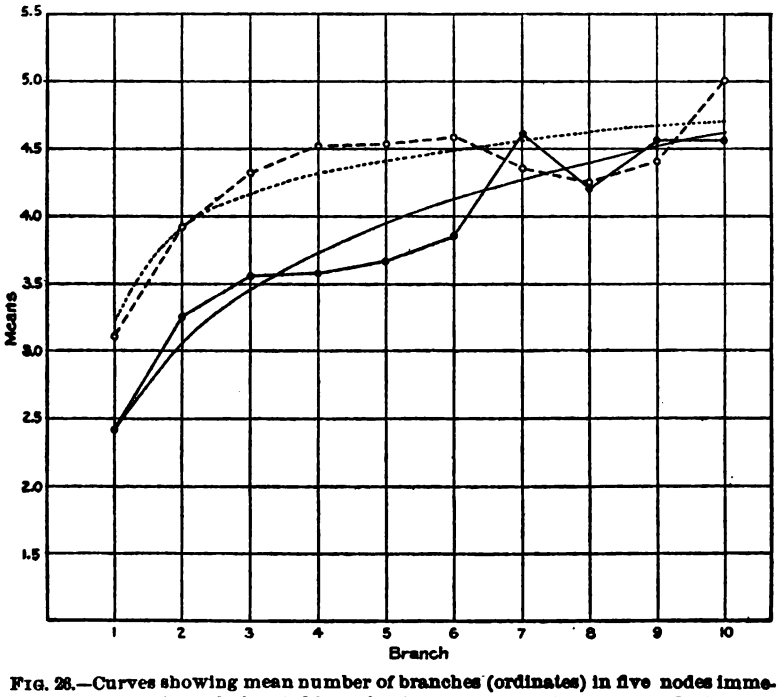

FIG. 26.—Curves showing mean number of branches (ordinates) in five nodes immediately following a designated branch (abscissas) on a primary axis. Series I, II, and III combined ————; Series IV ····· .

The numbers with which we are dealing here are so small relatively that great regularity in the observations can not be expected. There can be no doubt, however, that the general trend of the observations is adequately represented by the logarithmic curves. This means that the growth processes concerned in branch production, so far as may be judged from our present material, follow a logarithmic law. The mean number of branches formed in a constant number of nodes (5) increases

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the farther out on an axis we proceed, but the rate of increase varies inversely as the distance from the proximal end of the system. We thus get further evidence, from an entirely different source, of the generality of our first law of growth in Ceratophyllum. *The data furnish positive evidence that branch production and leaf production by the growing plant follow the same law.*

SUMMARY.

A study of branch production leads to the conclusion that "as the plant grows it tends with ever-increasing certainty to produce a branch at each node." In other words, as an axis of the plant grows longer the morphogenetic processes concerned in the production of lateral branches work, so to speak, more smoothly, and attain their results with greater regularity and constancy. But this is precisely the same conclusion to which we came with reference to the production of leaf-whorls (p. 106, *supra*). It was there shown that the leaf-number per whorl approaches more and more closely to a constant value the longer an axis grows. Putting both sets of results together, we now see that the plant as it grows tends to produce one or more branches and a constant number of leaves at each node. When a bud begins its growth it does not do either of these things with anything approaching certainty or regularity, but the longer it grows the more regular do the results become, until finally they are almost mathematically precise. Objectively it "profits by its experience" just as does an animal in its behavior. The results which have been obtained in this section of the paper show *that our two laws of growth* (pp. 88 and 106 *supra*) *operate in branch production as well as in leaf production.*

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GENERAL DISCUSSION OF RESULTS.

In bringing this paper to a close it appears desirable to discuss to some extent certain general aspects of the work as a whole, and to consider them on the theoretical side. Speaking broadly, the most significant result of this work appears to the writer to lie in the fact that, proceeding by quantitative analytical methods, it has been possible to formulate two laws of growth, which serve to describe with a very high degree of (*a*) precision, (*b*) completeness, and (*c*) generality the observed results of those processes of morphogenesis which in the growing Ceratophyllum plant lead to differentiation of parts. Further, it has been shown by direct appeal to statistics that the characteristic features of the variation of Ceratophyllum are obviously the result of the fact that the organism grows in accordance with these laws. By this, of course, is not meant that any kind of "explanation" of the origin of variation in Ceratophyllum has been gained. What has been gained, though, is the knowledge that, so far as our present material, which includes a reasonably wide range of conditions as to habitat, time of collection, etc., is concerned, the difference between two sets of individuals in respect to their variation constants are capable of practically complete interpretation solely in terms of the two laws of growth. The results actually observed are such as would be expected to arise in a system differentiating in accordance with our two growth laws.

The first of these laws of growth was stated on page 88 in the following way: "The mean number of leaves per whorl increases with each successive whorl, and in such a way that not only does the absolute increment diminish, but also the rate of increase diminishes, as the ordinal number of the whorl measured from a fixed point increases." If we let y stand for number of leaves in the whorl, and x denote the position in a series of successively formed whorls, then we find that y is a simple logarithmic function of x as follows:

$$y = A + C \log (x - a)$$

where A, C, and a are constants. The leaf whorls become differentiated with growth according to a logarithmic law. Also, as was shown in the last section (p. 125), if we let y denote the number of lateral branches found in a given number of nodes, and x as before the position of these particular nodes in the whole series, again we find y a simple logarithmic function of x. So that, in general terms, we see that in Ceratophyllum growth, whether expressed in the formation of leaf whorls or of lateral branches, takes place in such a way that the product increases at the same proportionate rate that the logarithm of the position in the whole series of products increases.

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The second law of growth was stated in the following words (p. 106, *supra*): "As whorls are successively produced by a growing bud they are formed with ever-increasing constancy to their type, the ultimate limit towards which the process is tending being absolute constancy."

This means that there is a steady diminution of variability accompanying the repetition of the morphogenetic process of whorl production. As has been indicated in the preceding section of the paper, the same rule holds with reference to branch production.

The two laws evidently have one important point in common, namely, they both express the fact that the form or character of a structure produced at any point on the plant is in part directly related to or determined by the previous morphogenetic history of the individual. Successively formed structures develop in such a way that from a purely objective point of view it appears as if the growing point on any axis were influenced in its formative activities by the previous "experience" through which the protoplasm of which it is composed has passed. Especially is this true with respect to the phenomena embodied in the second law. As has been shown above (p. 107), in the detailed discussion of this law morphogenetic products are progressively "better" formed, that is, closer to type, with each successive production. The theoretical importance of the demonstration of such a law of morphogenesis is evident.

It is the belief of the writer that both of these laws which have been demonstrated for Ceratophyllum have a wide generality in other organisms. From considerations of space it is impossible here to present detailed evidence for this belief, but a few points may be very briefly mentioned. We may consider each of the laws separately. In attempting to form an idea as to how generally a logarithmic law holds in the growth of other organisms than Ceratophyllum, we are unfortunately met at once by the difficulty that there have been comparatively few quantitatively exact studies of growth ever made. Furthermore, it is to be noted that so far as is known to the writer, there has hitherto been no extended study of exactly the same phase of the growth problem as that with which we have here dealt. In the present investigation we have dealt with what may be called *intra-individual* or *organal* growth, that is, with the growth differentiation of a *series* of successively produced, generally "like" organs of the *same* individual. In contrast to this previous studies of growth have usually dealt with what may be called *individual* growth, that is, with the growth change in the *same* organ or character in successive stages of life history of the individual or individuals. The two points of view stand to each other in the same relation that intra-individual variation does to intra-racial variation.

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It seems somewhat remarkable that so important a matter for the understanding of many problems of morphology as is the study of post-embryonic growth from both of the points of view noted should have been so much neglected. On the botanical side there is a good deal of literature dealing with special phases of the subject, but for our present point of view most of this material has little direct bearing. On the zoological side the principal work is due to anthropologists who have studied post-embryonic growth in man. In this field the available evidence regarding individual growth, so far as it goes, appears to be in good accord with what we have found in Ceratophyllum for organal growth. Thus, for example, Pearson (:04) has shown that the growth in auricular height of the head in children follows a logarithmic curve, and in a recent memoir by Lewenz and Pearson (:04) it is stated that such a curve has been found to represent the growth changes in other characters. Probably the most thorough and in all respects the best study of growth in any other animal than man which has been published is the classical investigation of Minot ('91) on growth in the guinea-pig. Speaking of his statistics Minot (p. 148) says: "They demonstrate two fundamental facts: *First*, the rate of growth diminishes almost uninterruptedly from the time onwards when the animal recovers from the post-natal loss of weight; *second*, the diminution is rapid at first, but slower afterwards." It will be seen that these statements exactly agree with those we have made above for growth in Ceratophyllum. That is, it would appear that the "individual" growth of the guinea-pig follows a logarithmic law. A careful study of Minot's data indicates that this is in fact the case. There is a great need for special investigations of growth directed towards determining exactly the laws which the changes follow. From such investigations we may hope to get some idea of the extent to which a logarithmic law is general. In any event, it is clear that such a growth law is not entirely unique in Ceratophyllum. On the contrary one has been convinced by going over the older material available in the literature, which it would take too much space to cite in detail here, that a logarithmic law is probably very general for growth in both plants and animals,* and for "individual" as well as "organal" growth.

There can be no doubt that what has been found in Ceratophyllum with reference to the variation of repeated parts is simply an example

*It has doubtless occurred to the reader that this logarithmic law of growth superficially resembles in form the well-known Weber-Fechner law regarding the quantitative relation of stimulation and sensation, as it was formulated by Fechner. Unfortunately later research in physiological psychology has shown that Fechner's statement of the law either does not hold at all, or at most only in a very limited range of cases.

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in a single case of a very general and fundamental biological law. This law has been differently stated, according to the particular class of phenomena in which it is seen to be operating. Thus Jennings (:05), dealing with the facts of behavior, calls it the "law of the readier resolution of physiological states" and formulates it in the way which has already been quoted (p. 108). He gives a number of examples showing the evidence in favor of the law from the behavior of lower organisms and says (p. 485): "In view of the facts, it is probable that the law is a general one and that it will be demonstrated in some form for other lower organisms." He also suggests the probability that the essential principle embodied in the law will be found to operate in morphogenetic processes. Definite statistical proof that such is in fact the case has been given by the present paper. Possibly a word of explanation is necessary to bring out the fact that the essential principle in the law as stated by Jennings is the same as that which underlies our law of diminishing variability. This will be clear if we consider in a little more detail the facts of behavior which led to the formulation of the law from that point of view. By analyzing certain phenomena of behavior in detail, Jennings (*loc. cit.*, p. 481) shows that:

> In the lowest organisms we find individual adjustment or regulation on the basis of the three following facts:
>
> (1) Definite internal processes are occurring in organisms.
>
> (2) Interference with these processes causes a change of behavior and varied movements, subjecting the organism to many different conditions.
>
> (3) One of these conditions relieves the interference with the internal processes, so that the changes in behavior cease, and the relieving condition is thus retained.
>
> * * *
>
> Now an additional factor enters the problem. By the process which we have just considered, the organism reaches in time a movement that brings relief from the interfering conditions. This relieving process becomes fixed through the operation of a certain law which appears to hold throughout organic activities. This law may be stated as follows: An action performed or a physiological state reached is performed or reached more rapidly after one or more repetitions, so that in time it becomes "habitual."

While, as Jennings points out, this statement of the law is not entirely adequate, yet it emphasizes the point at which comparison between the facts of behavior and morphogenesis may most easily be made. If in the production of successive whorls on an axis of a Ceratophyllum plant the variation about the type for each whorl diminishes, while, as has been shown, the type of the whorls changes at an ever-decreasing rate, it merely means that the production of a *particular type* of whorl tends, speaking in purely descriptive terms, to become "habitual." In both the psychological and morphogenetic cases there is a tendency to produce

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a stereotyped result with ever-increasing precision and constancy. Again, to take another example, it is obvious, as Jennings has pointed out, that "the operations of this law are seen on a vast scale in higher organisms, where they constitute what we commonly call memory, association, habit, and the basis of intelligence." If we consider for a moment the case of memory in man, it will be still further clear that there is objectively a fundamental similarity between one characteristic of this psychological phenomenon and such facts of morphogenesis as we have detailed for Ceratophyllum. Suppose a man sets to work to memorize a number of lines of poetry, and tests his acquirements by attempting to repeat the lines after each successive reading. The result will be something like this: When he attempts to repeat the lines after the first reading he will make a number of mistakes, or "deviations from the type" which is given by the exact text. On repeating the extract after the second reading the number of "errors" or "deviations" will tend to be fewer; after a third reading still fewer, and so on until finally there are no "deviations," or, in other words, the "type" is reproduced exactly at each successive repetition. Now, what do we find in Ceratophyllum? When the first whorl on an axis is produced we see, if we examine a large number of such whorls, that deviations from the type are produced relatively very frequently; second whorls exhibit a smaller number of such deviations; third whorls a still smaller number, and so on until we reach a condition of minimum variability, or in other words, a condition in which the type is produced each time with great precision and constancy. What goes on in the case of the memorizing and in the case of the growing plant may be objectively described in the same terms, the principal difference being that in the former example the type is absolutely fixed and constant, while in the latter it changes slowly. These illustrations will suffice to show that what we have called the law of diminishing variability operates in psychological as well as morphological phenomena.

In attempting to determine how generally this law of diminishing variability holds in respect to processes of growth, one is met as before with the difficulty that there have been but few investigations which have brought to light direct evidence on this point. It should be kept in mind that the conditions under which we should expect this law to show its operation in the clearest and most unequivocal form are those in which we have the production of a series of not greatly differentiated parts or characters. Obviously these conditions are best realized on the botanical side in plants having a type of structure similar to that of Ceratophyllum, and on the zoological side in animals built up on a simple metameric plan. So far as the writer knows, no systematic investiga-

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tion of the comparative variability of a series of metamerically repeated and slightly differentiated organs or characters in an animal form has ever been made. Hence it is hopeless at present to look to this source for confirmatory evidence for the law. On the botanical side the situation is somewhat better. Thus, for example, in a recent study of "Stages in the Development of *Sium cicutæfolium*" Shull (:05) has investigated the relative variability of the successive "nepionic" leaves in this form. In his fig. 1 (p. 9) he gives the frequency polygons for variations in the first eight leaves. These polygons very obviously substantiate his conclusion that "there is a progressive lessening of the variability from the first leaf onward." In this case we clearly have a direct confirmation of the law of diminishing variability. Similarly, in the papers of Cushman (:02, :03, and :04) there are several statements which appear to indicate that in many of the large number of plants studied by this worker the variation diminished in successive nepionic leaves. In a less direct way the operation of this law is to be seen, I believe, in a wide variety of morphological phenomena, including particularly what we have called above "individual" growth. Thus we have one example of it in the well-known fact that embryonic characters are much more variable than adult characters. That this is true has been directly proven by an elaborate system of measurements on duck embryos made some years ago by Fischel ('96).

Minot found the same thing in his guinea-pig measurements. On this point he says (*loc. cit.*, p. 140):

> This diminution of variability with age is demonstrable in the growth of other mammals, hence it probably occurs in all. We are led by this to put the question whether all variability of higher animals does not lessen with the age of the individual. In view of the extreme variations of structures which occur in all vertebrate embryos, and which, as all embryologists know familiarly, are far greater and more frequent than the variations of the adult, we are justified in asserting that there is a diminution of variability with age.

More evidence in the same direction might be cited, but it is unnecessary. If what has frequently been asserted should be proven by exact measurements, namely, that phylogenetically "young" organs are more variable than "old" organs, this again would fall in line with the general law of diminishing variability. It has recently been shown by Shull (:05*a*) that mutant forms of Œnothera are more variable than the parent form. One might hazard the suggestion that this fact is another expression of the operation of this same law. The matter could easily be tested by a biometrical investigation of mutants and their descendants extending through a considerable period of time.

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Purely as a working hypothesis, to be tested and limited by further investigation, the law of diminishing variability may be stated in the most general form to cover the facts in different fields, as follows: *In a continuous series of biological phenomena in which the same or homologous processes are repeated, the variation exhibited in the results of these processes diminishes with successive repetitions.*

In the opinion of the writer any attempt to develop a detailed theoretical explanation of *why* the two laws of growth which we have found in Ceratophyllum come to operate, would at present be premature. Just now there is a much greater need for quantitatively definite facts than for theories in the field of morphogenesis. What is, however, of great importance on the theoretical side is to see exactly the nature of the fundamental problem on which the interpretation of these growth laws depends. We have seen that there is a definite functional relation between the morphogenetic activity of a growing bud at any given time and its previous activity or "experience." In what way this functional relation is brought about is the fundamental problem which lies before us if we are to interpret our laws of growth. It will probably have occurred already to the reader that our results are a very clear cut example of the general principles which Semon (:04) has recently developed at great length. The influence of earlier upon later whorl production might very well be described as the result of "engrammatic" action on the bud in the formation of first and succeeding whorls. In fact, the whole of our results seem to form a most striking and complete illustration of the working out of Semon's principles in a particular case of ontogeny. But one can not escape the feeling that to attempt to interpret the facts in this way is simply to redescribe them in a new terminology without any substantial gain. Semon's rather obvious argument to meet such a criticism, which he of course foresees, that all science is only description, does not adequately remove the difficulty. What we require in cases like that with which we are here dealing is a description *in terms of known physiological principles*, and this the "mnemnic" terminology does not seem to provide. It seems to the writer that a more promising hypothesis on the basis of which to interpret such morphogenetic phenomena as those which have been set forth for Ceratophyllum might be developed along the lines suggested in recent papers by Holmes (:04) and Schiefferdecker (:04). Such an interpretation has been worked out by the writer for use as a working hypothesis in further investigations in this field which are now in progress, but until it has been tested it hardly seems worth while to publish it.

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Finally, in closing, I desire to emphasize the great importance in any study of variation of the analysis of the *intra-individual* variability of the characters which are to form the basis of intra-racial investigations. We have seen in a repeated character of the same individual a whole series of variation constants appearing in an orderly manner and representing degrees of variation from practically zero up, degrees of skewness from positive through symmetry to negative, etc. It is obvious that on any problems of intra-racial variation we could with Ceratophyllum get widely divergent results by taking whorls from different parts of the plant. Ordinarily when an investigation of a problem of geographical variation, or of natural selection, or of almost any phase of intra-racial variation is made on the basis of characters like the leaf-whorls of Ceratophyllum, only a few are taken from each individual. Either no attention at all is paid to differentiation in the characters, or at most only the characters in the immediate neighborhood of those chosen are examined, and if there is no differentiation easily detectable among them, the conclusion is reached that any factor of this kind may be neglected. It seems to me that the results of the present paper show that the question of whether or not there is a differentiation *within* the character group chosen for investigation is not necessarily the important thing at all. If one takes the 10 most distal whorls on Ceratophyllum plants, there is substantially no differentiation in respect to leaf-number. Yet, to conclude, when this had been ascertained by superficial examination, as it could be, that these whorls, since they were undifferentiated and therefore could be considered homogeneous material, might be taken to represent the conditions of the individual as a whole in an intra-racial investigation, would lead to absolutely fallacious results. It is true that there is no marked differentiation among these distal whorls, but the very reason that there is not is that a perfectly definite and orderly process of differential development has led as an end result to the continued production of substantially the same type of whorl, regardless of environment or other influences. These whorls are not greatly differentiated, but neither are they truly representative of the individual. If characters of this kind are to be used as the basis of investigations of problems of intra-racial variability, it clearly is absolutely necessary that the laws according to which the characters are differentiated during the development of the individual must first be ascertained if valid results are to be obtained. When this has been done we may turn to intra- and inter-racial problems, and, using the methods which have been developed by Pearson for dealing with differentiated characters, hope to reach definite conclusions.

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GENERAL SUMMARY.

This paper deals with a biometrical analysis of intra-individual variability and differentiation in Ceratophyllum. The characters principally dealt with are (*a*) the number of leaves in the whorl; (*b*) the position of the whorl on the plant; (*c*) the size of the various divisions of the plant; and (*d*) the position of branches. Some of the chief *results* as to fact may be summarized as follows:

(1) Dealing with the intra-individual variation in leaf-number per whorl it is found that the whorls borne on the different axial divisions of the plant (main stem, primary, secondary, etc., branches) are distinctly differentiated in respect to both type and variability.

(2) The mean number of leaves per whorl is highest in the whorls on the most central division of the plant (the main stem) and decreases regularly as we pass to more peripheral divisions.

(3) The whorls on the main stem are the least variable in leaf-number, and the variation increases regularly in the more peripheral divisions, till a maximum is reached in secondary-branch whorls. The variation then tends to diminish in the whorls on higher-order branches.

(4) More than half of the total number of whorls are borne on primary branches. Of the remaining whorls somewhat more are borne on secondary branches than on the main stem. Tertiary and quaternary branches bear relatively few whorls.

(5) Primary branches are absolutely and relatively more variable in size than are secondaries.

(6) There is a relatively high degree of correlation between the number of leaves in the whorl and its position on any axis of the plant.

(7) The degree of this correlation is lowest in the most central division of the plant (main stem) and increases as we pass to the more peripheral divisions.

(8) The regression of leaf-number on position is not linear, but logarithmic.

(9) This leads to what we have called the "first law of growth" in Ceratophyllum, which may be stated as follows: On any axial division of the plant the mean number of leaves per whorl increases with each successive whorl in such a way that both the absolute increment and the rate of increase diminish as the distance (in units of nodes) of the whorl from a fixed point increases.

(10) Branches which show an excess (or defect) from the average in the number of leaves in the first whorl tend to have the succeeding whorls greater (or less) than their respective averages. This tendency diminishes as we go distad on the plant.

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(11) On any axial division of the plant as whorls are successively produced by a growing bud they are formed with ever-increasing constancy to their type. This we have called the "second law of growth in Ceratophyllum." The growing-point appears to be influenced in its morphogenetic activity by its previous experience.

(12) These two laws operate in branch production as well as in leaf production in Ceratophyllum.

Summarized statements of the detailed results and discussions of the *conclusions* drawn from them will be found on pp. 26, 54–57, 88–92, 95, 106–108, 115, and 124 and need not be repeated here.

The results of this study emphasize the necessity for a knowledge of the laws of differentiation within the individual of characters as a preliminary to the use of these characters in the study of the problems of evolution.

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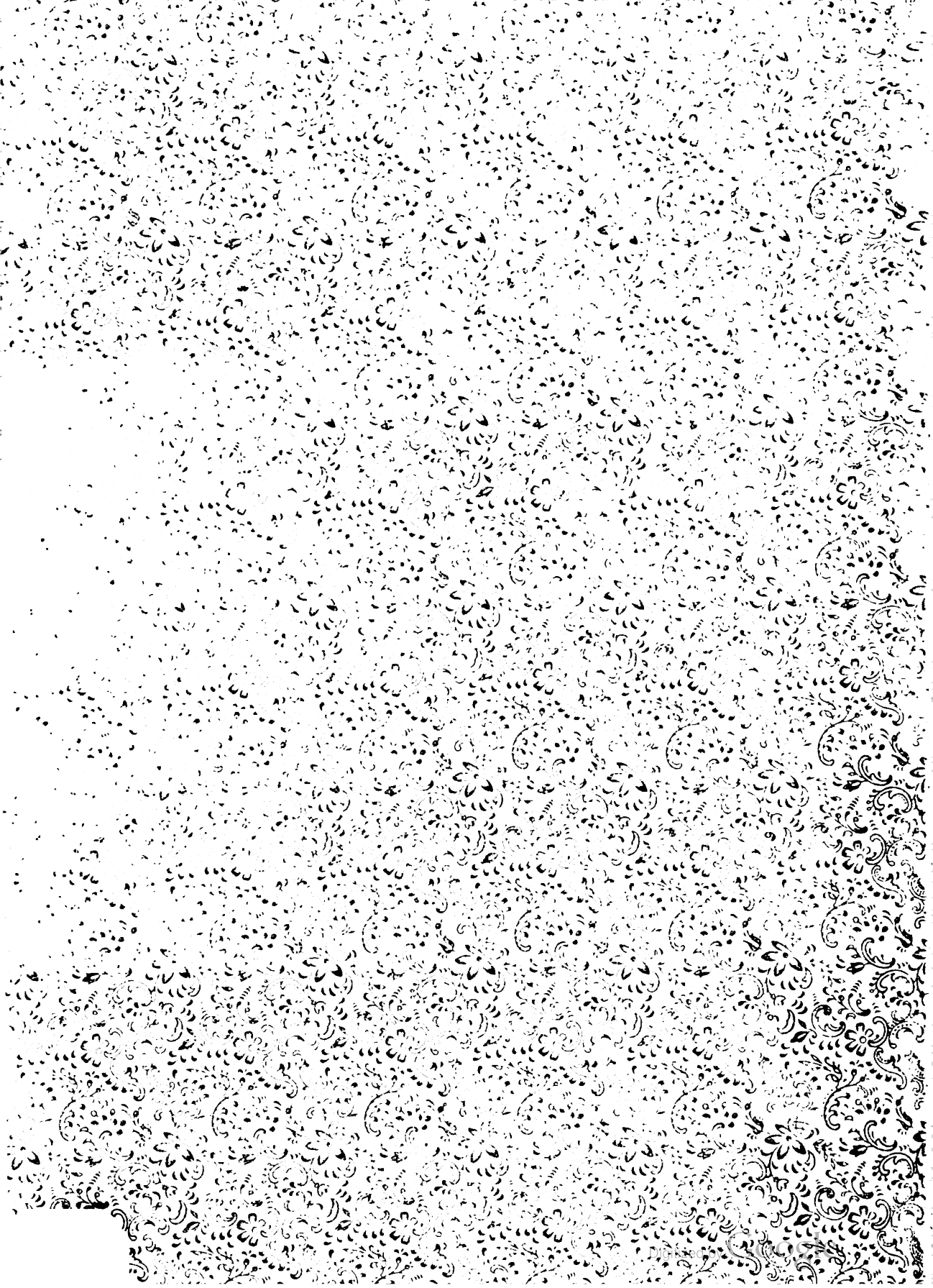
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